JOURNAL
OF THE
FISHERIES RESEARCH BOARD
OF CANADA

Volume 20, No. 5

OHIO STATE UNIVERSITY
DEC 16 1963
LIBRARY

CONTENTS

PAGES

PICKARD, G. L. Oceanographic characteristics of inlets of Vancouver Island, British Columbia..... 1109–1144

TOMLINSON, N., R. E. E. JONAS AND S. E. GEIGER. Glycolysis in lingcod muscle during frozen storage 1145–1152

DYER, W. J., D. I. FRASER AND S. N. TIBBO. Composition and palatability of porbeagle flesh..... 1153–1158

PITT, T. K. Vertebral numbers of American plaice, *Hippoglossoides platessoides* (Fabricius), in the Northwest Atlantic..... 1159–1181

TOMLINSON, N., AND S. E. GEIGER. Brine spray frozen cure. Sodium, potassium, lactic acid and acid-soluble phosphorus in the muscle, and the influence thereon of thawing and precooking..... 1183–1187

SCOTT, W. B., AND W. J. CHRISTIE. The invasion of the lower Great Lakes by the white perch, *Roccus americanus* (Gmelin)..... 1189–1195

BELL, W. H., AND N. BOSTON. Tidal calibration of the Hecate Model..... 1197–1212

MUIR, BARRY S. Vital statistics of *Esox masquinongy* in Nogies Creek, Ontario. I. Tag loss, mortality due to tagging, and the estimate of exploitation... 1213–1230

(*Continued overleaf*)

OTTAWA
SEPTEMBER
1963

MacCallum, W. A., M. W. Mullan and Isabel N. Plaunt. Factors influencing the effectiveness of fresh fish washing operations 1231–1244

Pemberton, A. T., and C. W. Andrews. Effect of photoperiods on the reactions of juvenile Atlantic salmon (*Salmo salar* L.) to light stimuli 1245–1266

Scattle, D. H. Pollock (*Pollachius virens* (L.)) in the Bay of Fundy 1267–1314

Hedgpeth, Joel W. Pycnogonida of the North American Arctic 1315–1348

Obituary — Edith Berkeley. By W. A. Clemens 1349–1352

NOTES

An occurrence of mako sharks, *Isurus oxyrinchus*, Rafinesque 1810, in the Canadian Atlantic. By S. N. Tibbo, R. A. McKenzie and W. B. Scott .. 1353–1354

Editor:
J. C. Stevenson

Associate Editor:
F. G. Bligh

Fisheries Research Board of Canada
Sir Charles Tupper Building
Ottawa, Ont., Canada

Manuscripts for publication should be addressed to the Editor

ROGER DUHAMEL, F.R.S.C.
QUEEN'S PRINTER AND CONTROLLER OF STATIONERY
OTTAWA, 1963

Oceanographic Characteristics of Inlets of Vancouver Island, British Columbia[1]

By G. L. Pickard

Institute of Oceanography
University of British Columbia, Vancouver, B.C.

ABSTRACT

Observations of temperature, salinity and dissolved oxygen content in all but one of the inlets of ten or more miles in length along the west coast of Vancouver Island were made by the University of British Columbia in 1959 and some additional observations were made in 1960 and 1961. The data are summarized to provide a general picture of the oceanographic characteristics of fifteen inlets. Attention is drawn to various features, and comparisons are made with the previous data which are available for only five of the inlets here described. Comparisons are also made with inlets in the mainland coast of British Columbia previously described by Pickard in 1961 in the Journal of the Fisheries Research Board of Canada.

Generally the Vancouver Island inlets are shorter and shallower than those of the mainland coast and have shallower sills. The river runoff into the inlets is considerably less than into the mainland ones and has a winter maximum in contrast to the summer maximum on the mainland.

Surface salinities during the summer in 1959, 1960 and 1961 were in most cases between 12 and 28‰ at the inlet head increasing to 27–31‰ at the mouth, while surface temperatures were between 10 and 15°C. The low-salinity surface layer had a thickness of 2 m or less in all but two cases. Secchi disc depths were usually from 4 to 8 m. The deep water characteristics were from 7.5 to 9.5°C and 31 to 33.6‰ except in the Clayoquot Sound group where the water was warmer (to 15.4°C) and less saline (to 24.8‰). Dissolved oxygen values were very variable even along individual inlets. At depths greater than 100 m the content was usually less than 4 ml/l and in many cases less than 1 ml/l. The effect of the shallow sills in limiting deep water circulation appeared to be significant.

Even when all the available data are assembled there are no time series of observations sufficient to prepare a description of seasonal variations of water properties, but data for six years from 1939 to 1961 are available for Alberni Inlet and for three years for the Nootka Sound inlets and for Neroutsos Inlet. These data indicate that in the deep water changes of up to 0.4‰ in salinity, 1 C° in temperature and 2.5 ml/l in dissolved oxygen content may occur from year to year.

An hypothesis is advanced that, on account of the relatively shallow sills of many of the inlets, the deep water in their basins forms a 'memory' of extreme (high density) conditions of the continental shelf waters outside the inlets, and that the consistency of the basin water characteristics in the inlets suggests that the water properties observed in the shelf waters in 1959–61 by the Pacific Oceanographic Group may be typical of shelf waters in this region over many years.

[1]Received for publication May 9, 1962.

J. Fish. Res. Bd. Canada, **20**(5), 1963.
Printed in Canada.

CONTENTS

PAGE

ABSTRACT ... 1109

1. INTRODUCTION ... 1110

2. GENERAL CHARACTERISTICS
- 2.1 Inlet dimensions ... 1113
- 2.2 Bottom materials ... 1116
- 2.3 Freshwater runoff into the inlets ... 1116

3. SALINITY AND TEMPERATURE
- 3.1 Surface salinity and temperature distributions ... 1118
- 3.2 Subsurface salinity and temperature distributions ... 1120
  - 3.21 Salinity–depth profiles ... 1124
  - 3.22 Temperature–depth profiles ... 1127

4. DISSOLVED OXYGEN ... 1129

5. WATER TRANSPARENCY IN THE SURFACE LAYER ... 1131

6. DISCUSSION
- 6.1 Temperature–salinity characteristics ... 1131
- 6.2 Source of deep water and effect of outer sill depth ... 1131
- 6.3 Periodic changes ... 1135
  - 6.31 Alberni Inlet ... 1135
  - 6.32 The Nootka Sound inlets ... 1138
  - 6.33 Neroutsos Inlet ... 1140

7. SUMMARY ... 1142

8. ACKNOWLEDGMENTS ... 1143

9. REFERENCES ... 1143

1. INTRODUCTION

THE COAST of British Columbia is indented by a number of long and relatively narrow bodies of water opening to the sea at one end and in most cases having rivers running into them. On the charts these indentations are variously and unsystematically named "inlet", "sound", "channel", etc. For convenience, the term "inlet" will be used as a generic name in the following discussion.

As a continuation of the study of these coastal inlets by the Institute of Oceanography, University of British Columbia, an oceanographic survey of a number of those along the west coast of Vancouver Island was made in 1959 with limited observations in 1960 and 1961. The purpose of the present paper is to extend the information presented by Pickard (1961) for the mainland coast inlets by a description of some of the oceanographic characteristics of all the Vancouver Island inlets of ten or more miles in length. The term 'Vancouver Island inlets' as used in this paper refers to those in the west or Pacific coast of the Island (Fig. 1) and does not include Saanich Inlet (which has been described by Herlinveaux, 1962) in the southeast coast.

The shape and location of these inlets and the inflow of fresh water which gives rise to a low-salinity surface layer identifies them as estuaries in the sense in which the term is currently used to describe a "semi-enclosed body of water having a free connection with the open sea and containing a measurable quantity

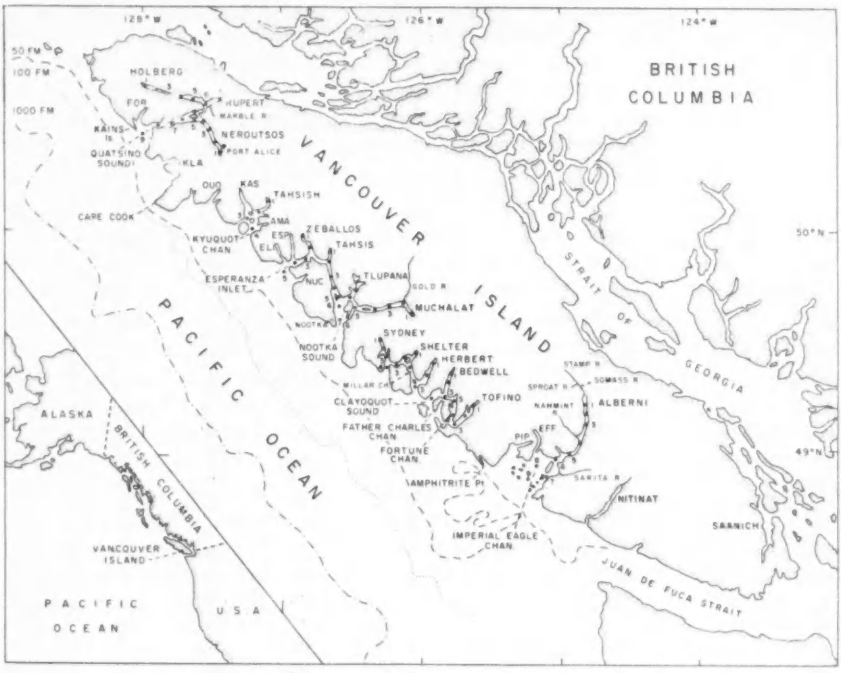


FIG. 1. Vancouver Island, British Columbia, showing main inlets.

of sea salt" (Pritchard, 1952, p. 245). A characteristic of this type of estuary is that the low-salinity surface layer has a net motion to seaward. As it moves this layer picks up saline water from below and eventually carries it out of the estuary. To maintain continuity of volume there must be a subsurface inflow of saline water. This pattern of surface outflow and subsurface inflow is referred to as an "estuarine circulation". According to Defant (1961, Vol. 1, p. 538) this type of circulation was described by F. L. Ekman in 1875 and a theoretical study was made by V. W. Ekman in 1899. More recently the estuarine circulation was described and discussed in detail by Tully (1949) for Alberni Inlet, while Pritchard (1952) reviewed some of the studies of estuaries.

In the examination of the mainland inlets the conclusion was drawn (Pickard, 1961) that the river runoff into them not only helped to determine the water property distributions in the surface layer but also influenced the deep water properties by the extent to which it induced the subsurface inflow as a part of the estuarine circulation. For example the mainland inlets with small river runoff generally had lesser and more variable dissolved oxygen contents, attributed to less rapid inflow and circulation of subsurface water, than those with large river runoff. The possibility that river runoff would be found to exert a similar effect in the Vancouver Island inlets was expected.

TABLE I. Salient dimensions of the inlets of five miles length or more along the west coast of Vancouver Island, British Columbia.

Name	Abbreviation	Length	Mean width	Mean mid-inlet depth	Maximum depth	Outer Sill depth (Note 1)	Notes
		Nautical Miles		*m*	*m*	*m*	
Holberg Inlet	HOL	18.5	0.7	80	170	18	2
Rupert Inlet	RUP	5.5	0.95	110	165	18	2
Neroutsos Inlet	NER	32	1.2	150	245	78	3
Forward Inlet	FOR	6	0.6	30	65	none	
Klaskino Inlet	KLA	6	0.4	35	65	18	
Ououkinsh Inlet	OUO	7.5	0.65	85	120	60	
Kashutl Inlet	KAS	8.5	0.95	110	225	none	4
Tahsish Inlet	TAHH	15	0.9	185	265	60	
Amai Inlet	AMA	5.5	0.55	105	215	none	
Port Eliza	ELI	6	0.35	50	60	38	
Espinosa Inlet	ESP	7.5	0.7	215	275	220	
Zeballos Inlet	ZEB	16	0.95	195	240	28	5
Nuchalitz Inlet	NUC	8	0.7	25	75	10	
Tahsis Inlet	TAH	21	0.65	135	210	50	6
Tlupana Inlet	TLU	10	0.8	200	265	180	7
Muchalat Inlet	MUC	26	0.8	220	385	50	8
Sydney Inlet	SYD	11	0.7	80	140	24	9
Shelter Inlet	SHE	10	0.7	115	175	24	9, 10
Herbert Inlet	HER	12.5	1.1	100	150	8	
Bedwell Sound	BED	18	1.0	50	90	12	11
Tofino Inlet	TOF	21	0.75	70	150	12	12
Pipestem Inlet	PIP	5	0.4	45	70	34	
Effingham Inlet	EFF	9	0.65	95	205	56	
Alberni Inlet	ALB	37	0.7	145	365	88	13
Nitinat Lake	NIT	12.5	0.6	140	205	2	14

Notes:

1. All depths are measured relative to chart datum at lowest normal tides; extreme tides may increase the values by 5 m.
2. Holberg and Rupert taken to Quatsino Narrows.
3. Neroutsos with continuation along Quatsino Sound.
4. Kashutl taken to junction with Tahsish.
5. Zeballos with continuation along Esperanza.
6. Tahsis with continuation along Cook Channel to Nootka Sound. Inner sill of 57 m at Tsowwin Narrows in Tahsis.
7. To junction with Tahsis.
8. Muchalat with continuation along Zuciarte Channel to Nootka Sound. Inner sill of 91 m depth in Muchalat.
9. Sydney and Shelter are connected by Millar Channel and Hayden Passage, the sill depth of which is 35 m.
10. To junction with Sydney, sill depth as for Sydney.
11. Bedwell and continuation along Father Charles Channel.
12. Tofino and Fortune Channel to junction with Bedwell. Inner sills of 24 m between Bedwell and Fortune, and of 33 m between Fortune and Tofino.
13. Alberni and continuation along Imperial Eagle Channel; mean width stated only for Alberni proper. Inner sill of 37 m depth at Sproat Narrows.
14. Nitinat Lake has a shallow entrance about 1.5 miles long with several sills. The outer bar is 2 m deep and three inner sills are about 3 m deep (at lowest normal tides). Depths in Nitinat were taken from a bathymetric chart prepared by Dr T. G. Northcote, Institute of Fisheries, University of British Columbia, from his thirteen echo-sounder cross-sections.

The previously published oceanographic information on the Vancouver Island inlets is essentially limited to that for the Nootka Sound inlets (Tully, 1937), Alberni Inlet (Tully, 1949; Anon., 1957; and Waldichuk, 1956), and Neroutsos Inlet (Waldichuk, 1958). A brief manuscript report on Quatsino Sound (Neroutsos Inlet section) was prepared by Hutchinson and Lucas (1927) and unpublished data on Alberni Inlet and Muchalat Inlet are in the files of the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C. (Dr M. Waldichuk, private communication).

Nitinat Lake toward the southeastern end of the west coast of Vancouver Island has, despite its name, communication with the sea and is an estuarine inlet with a very shallow sill. Dr T. G. Northcote, of the Institute of Fisheries of the University of British Columbia, has made measurements of depth along the inlet, and of water properties at the head and mouth in it and has kindly permitted a summary of his observations to be included in the present paper in advance of his own publication of them.

The oceanographic stations occupied in 1959, 1960 and 1961 were at intervals of three to five miles and were located as far as possible in straight, deep reaches. It should be noted that the station numbers for the Vancouver Island inlets start with Sta. 1 at the inlet head, the opposite arrangement to that used for the mainland coast inlets. The data are available in the form of Data Reports of the Institute of Oceanography, University of British Columbia for the individual cruises (Anon., 1959, 1960b, 1961).

2. GENERAL CHARACTERISTICS

2.1 Inlet Dimensions

Charts have been published (Anon., 1962a) for the whole of the west coast of Vancouver Island, and these were used in determining the dimensions of the inlets of five or more miles in length. These dimensions are listed in Table I and longitudinal profiles are given in Fig. 2 and 3. Fig. 8A is a longitudinal section of Nitinat from Northcote's measurements.

Some of the inlets occur in groups with a common opening to the sea or as a large inlet with side arms. In many cases a single body of water bears different names for different parts of its length. For convenience in this paper such bodies are referred to by the name of their inland portion (e.g. Alberni, Tofino, Neroutsos).

The inlets in the west coast of Vancouver Island are generally shorter, narrower and shallower than those in the mainland coast. Alberni is the longest (37 nautical miles, 69 km) while average widths range from 0.4 to 1.2 miles (0.7 to 1.9 km). The average depth is about 125 m while the maximum is 385 m in Muchalat. The sills are generally shallower than in the mainland inlets. In a number of cases the outer sill is on the continental shelf several miles outside the mouth of the inlet. Many inlets also have inner sills which divide them into a series of basins.

It should be noted that the depth data in Table I taken from the Canadian Hydrographic Service charts represent depths below lowest normal tides.

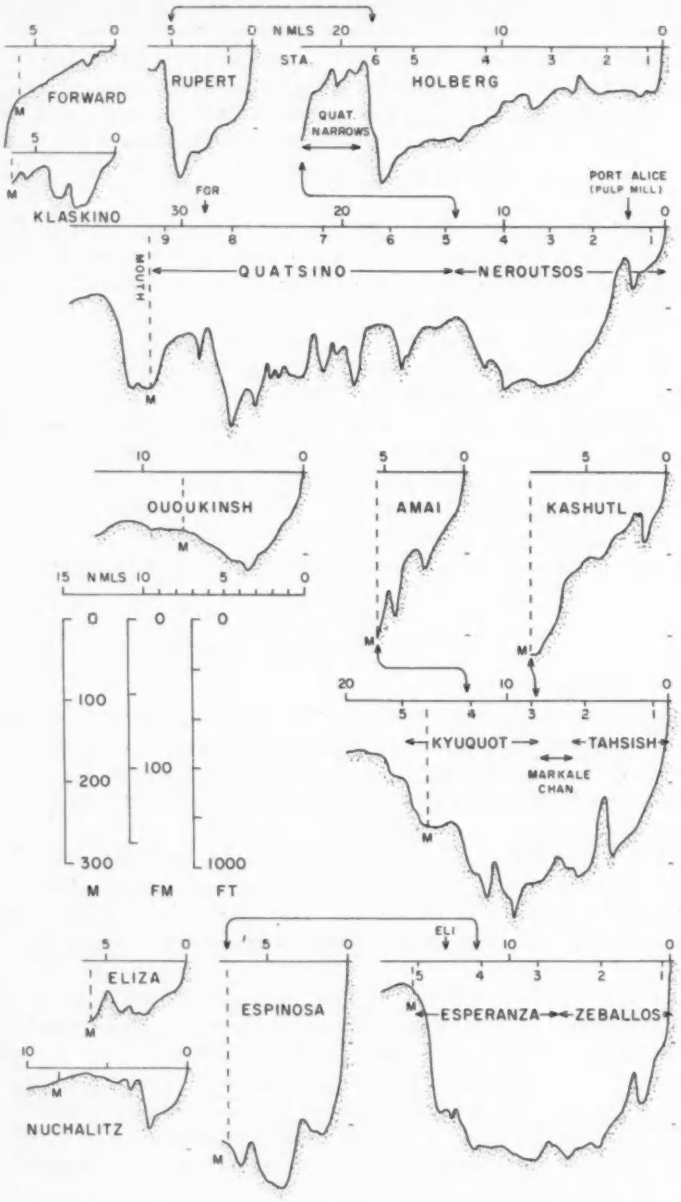


FIG. 2. Longitudinal sections along inlets of Vancouver Island, northern group from Holberg to Zeballos. ("M" indicates mouth of inlet.)

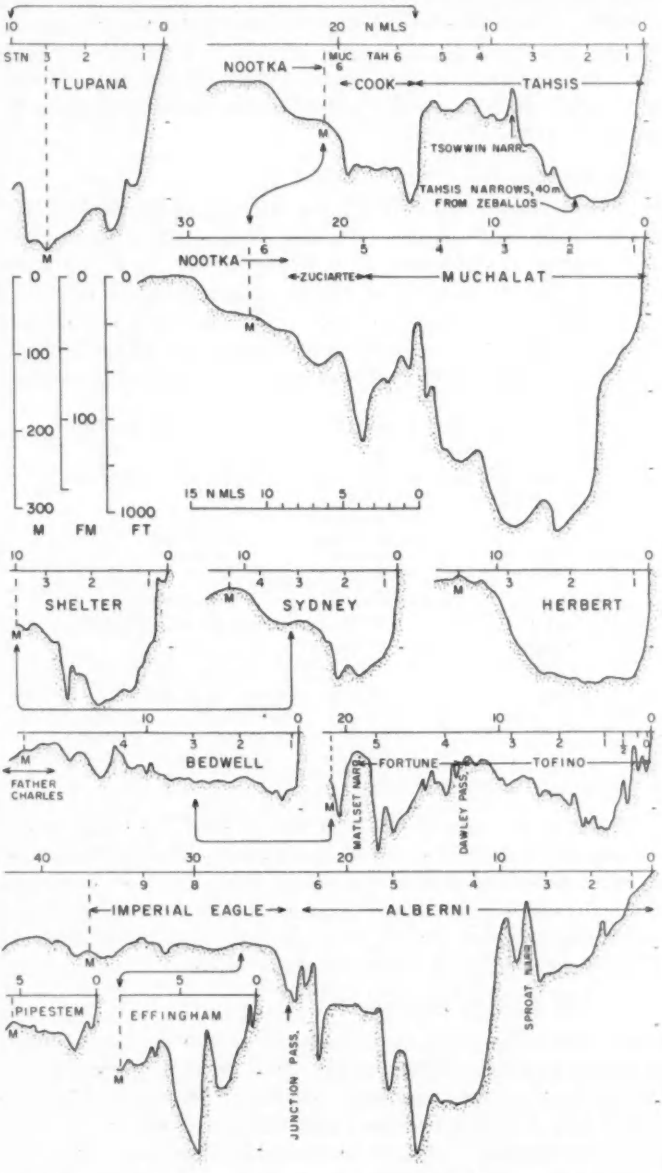


FIG. 3. Longitudinal sections along inlets of Vancouver Island, southern group from Tahsis to Alberni ("M" indicates mouth of inlet.)

Normal high tides raise the water level by about 4 m and extreme tides by 5 m (Anon., 1962b). The 'effective' sill depths (used in Section 6.2) for the inflow of ocean water are therefore taken to be greater by 4 m than the figures given in Table I. When preparing Fig. 2 and 3 most of the inner sill depths were determined from Canadian Hydrographic Service field sheets which have more detail than the published charts.

2.2 Bottom Materials

In 1959, casts were made with a LaFond-Dietz (1948) snapper at 50 of the 68 stations occupied, and samples obtained at 43 of them distributed approximately in proportion to the length of each inlet. Shipboard examination of the samples yielded the distribution of bottom material characteristics shown in Table II. At seven stations the snapper failed to close and no sample was obtained. It was judged that in each case this was because the bottom material was mud which was too soft to trip the closing mechanism of the snapper.

Table II. Characteristics of bottom materials in inlets of the west coast of Vancouver Island.

Material	Percentage of samples containing material	Consistency of mud	
Mud	90%	Firm (kept form)	40%
Sand	26%	Soft (flowed)	60%
Gravel	7%		
Shells	21%	*Colour of mud*	
Wood, twigs	14%		
		Black	20%
		Brown	60%
Smell of H_2S	16%	Brown-green	20%

The frequency of occurrence of mud and of sand is similar to that in the mainland inlets but shells and wood are more common in the Vancouver Island inlets, and the consistency is more frequently soft. A major difference is that while in the mainland inlets the bottom materials are predominantly grey (70%) because of the glacial flour content, those in the Vancouver Island inlets are predominantly brown. No grey samples were obtained.

2.3 Fresh Water Runoff into the Inlets

Published river-runoff data for the west coast of Vancouver Island (Anon., 1960a) are limited to those for the Somass River (formed by the combination of the Stamp and the Sproat Rivers) into the head of Alberni, the Nahmint River into the side and the Sarita River into the mouth of Alberni, the Gold River into Muchalat, and the Marble River into Rupert-Holberg. Monthly mean values of runoff are plotted as full lines in Fig. 4. It will be seen that all the rivers show a peak runoff in the winter while the Somass and the Gold have a second peak in May. The dashed lines in Fig. 4 show the monthly mean precipitation on the

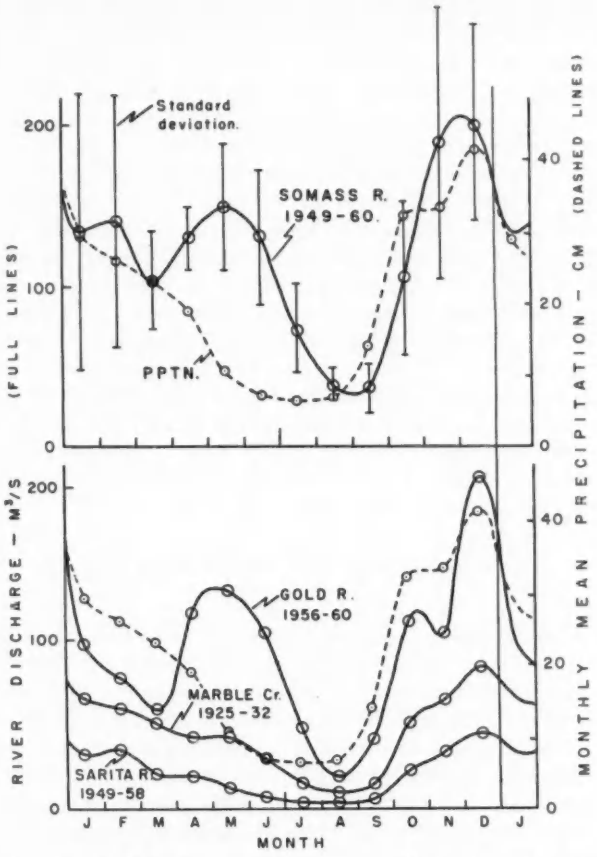


FIG. 4. Monthly mean runoff of four rivers flowing into inlets in Vancouver Island, and monthly mean precipitation typical of the west coast of Vancouver Island.

west coast of Vancouver Island from the 'General synopsis of temperature and precipitation' in the Monthly Record of the Meteorological Branch (Anon., 1955–60, p. 2).

For the Sarita River the winter runoff maximum corresponds in time to the winter maximum in precipitation. Lane (1962) pointed out that the Sarita River drains only the lower levels and suggested that its runoff pattern reflects the precipitation pattern in its neighbourhood. He used data for 1956 and 1957 to show a close correspondence between details of precipitation and runoff. The present Fig. 4 shows mean values over many years and much of the short term detail, such as is apparent in Lane's example, has disappeared but the general correspondence is still evident.

For the Somass and Gold Rivers the runoff during the period from April to July is higher than would be expected from the direct effect of precipitation. Lane attributed the May subsidiary maximum for the Stamp River (flowing into the Somass) to a contribution from snow-melt at higher elevations drained by this river. The writer agrees with Lane's explanation of the May maximum and assumes that a similar explanation applies to that for the Gold River.

It must be pointed out that there are very large year-to-year variations in monthly mean runoff. The magnitude of these is indicated by the standard deviations shown in Fig. 4 for the Somass River as an example.

For most of the rivers the runoff characteristics can be described generally as a large runoff from October to June with a peak in December, falling from July to September to one-fifth to one-tenth of the winter rate with a minimum in August or September. For the Somass and Gold Rivers there is a second runoff peak in May.

The two larger runoff rates illustrated are only one-quarter to one-eighth of those for the larger mainland coast inlets. In addition it should be noted that the summer *minimum* in river runoff in August or September on the west coast of Vancouver Island contrasts with the summer *maximum* in the June to September period in the mainland coast inlets.

3. SALINITY AND TEMPERATURE

3.1 Surface Salinity and Temperature

In Fig. 5 are shown the surface salinity and temperature values along the Vancouver Island inlets in May or June. It is seen that some of the inlets showed evidence of significant river runoff by low salinity values toward the head and a salinity gradient along much of the inlet length. The most notable were Alberni, Tofino, Muchalat, Tlupana and Neroutsos. With the exception of Shelter and Rupert, the remainder showed some decrease in the vicinity of the inlet head but the salinity values were greater than 10‰. In most inlets the surface salinity was nowhere less than 50% of the maximum (deep water) value in the inlet. In the case of Tofino, in 1959 an abrupt change of salinity was evident between stations Tofino 5 and Bedwell 3, these being separated by Matlset Narrows (Fig. 3), and possibly of both salinity and temperature between Tofino 3 and 4 through Dawley Passage (Fig. 3). In 1960 there was a large change of salinity between Tofino 3 and 4 but not of temperature, while the change through Matlset Narrows was small.

The only other region in the west coast of Vancouver Island where there is a shallow narrows in the length of an inlet system is between Holberg and Neroutsos through Quatsino Narrows (Fig. 2). Along Neroutsos there was a marked salinity and temperature jump between Neroutsos 4 and 5 where Neroutsos proper joins Quatsino Sound (Fig. 1). The salinity (23.06‰) at Holberg 6, i.e. on the Holberg side of Quatsino Narrows, was lower than that at the adjacent stations and there was no corresponding anomaly of temperature from the surroundings. However this value only represented a very thin layer as the salinity at 2 m depth was 29.04‰. It probably resulted from the outflow

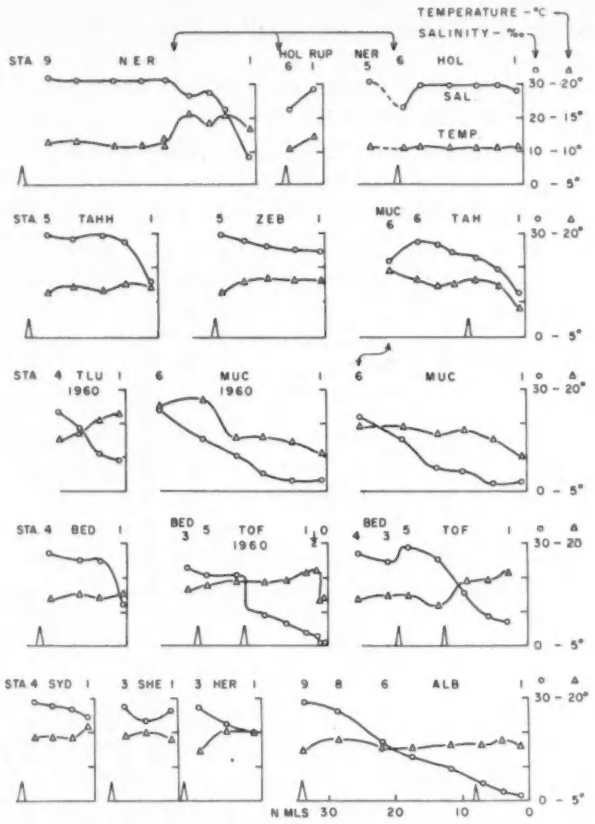

TEMPERATURE - °C
SALINITY - ‰
STA 9 N E R 1 HOL 6 RUP 1 NER 5 6 HOL 1
SAL
TEMP
30 - 20°
20 - 15°
10 - 10°
0 - 5°
STA 5 TAHH 1 5 ZEB 1 MUC 6 6 TAH 1
STA 4 TLU 1 1960 6 MUC 1960 6 MUC 1
STA 4 BED 1 BED 3 5 TOF 1960 BED 4 3 5 TOF 1
STA 4 SYD 1 3 SHE 1 3 HER 1 9 8 6 ALB 1
N MLS 30 20 10 0

FIG. 5. Surface temperature and salinity along inlets of Vancouver Island for 1959 (May), and for 1960 (June) where stated.

from the Marble River which enters near Holberg 6. This is an example of an unusual inlet in which the major freshwater runoff is at the mouth rather than at the head. Away from the mouth, the surface salinity and temperature in Holberg were unusually uniform.

In Nitinat the surface salinity in January 1959 increased from 2.0‰ near Sta. II at the head (Fig. 8A) to 3.0‰ near Sta. I inside the mouth, while in May 1959 it increased from 2.5 to 17.4‰ between the same positions. In June 1961 it increased from 6.9‰ at Sta. II to 11.4‰ at Sta. I.

In Fig. 5 it is shown that in the majority of inlets the surface temperature remained within ±1 C° of the mean value along the length of the inlet. In Holberg it remained within ±0.4 C°.

The exceptions were of two types. In Tahsis and Muchalat only, the temperature decreased to the head. In Tlupana there was an increase, while in Neroutsos and Tofino (in 1959) there was a sudden increase in surface temperature by about 4 C° in mid inlet. In Neroutsos this was at the junction between

Neroutsos proper and Quatsino Sound, while in Tofino it was at the narrows of Dawley Passage.

In Nitinat the surface temperature in June 1961 was 16.6°C at Sta. II near the head and 16.1°C at Sta. I inside the mouth.

3.2 Subsurface Salinity and Temperature Distributions

Figures 6 and 7 show typical vertical profiles of temperature, salinity and dissolved oxygen for all the inlets visited in 1959 and 1960, and Fig. 8B shows

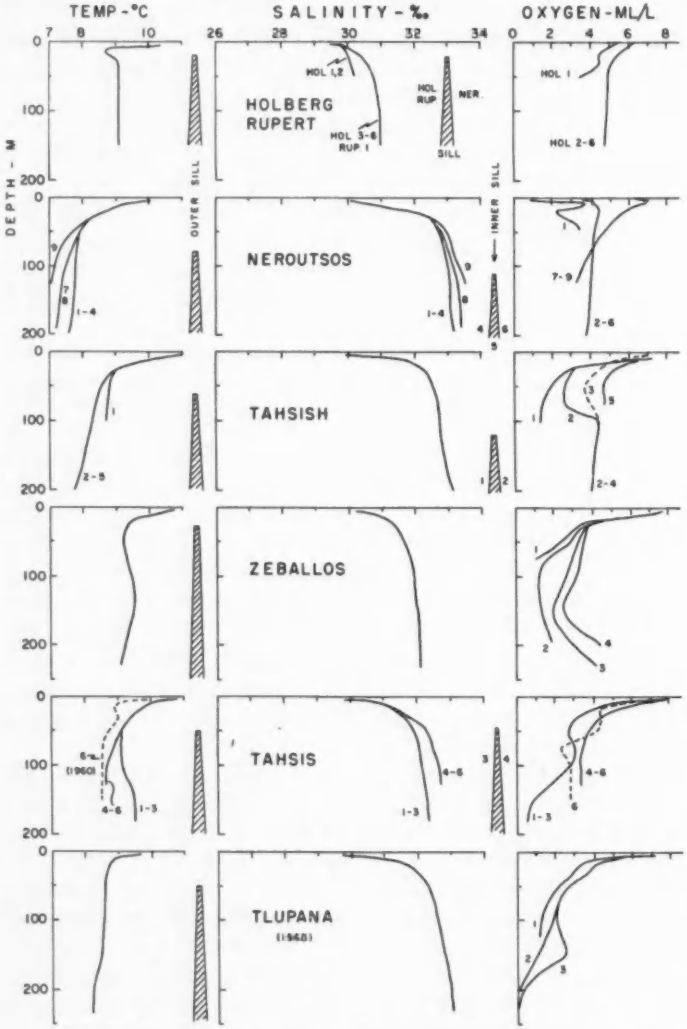


FIG. 6. Characteristic vertical profiles of temperature, salinity and dissolved oxygen for northern inlets in Vancouver Island from Holberg to Tlupana.

typical profiles for Nitinat from Northcote's data. For some inlets a single profile each for temperature and salinity is adequate to show the character of the distribution for the whole inlet, but for others it is necessary to present two or more profiles to show the difference between the waters in basins separated by sills. Figures 6 and 7 illustrate qualitatively the great variety of profiles found in these inlets.

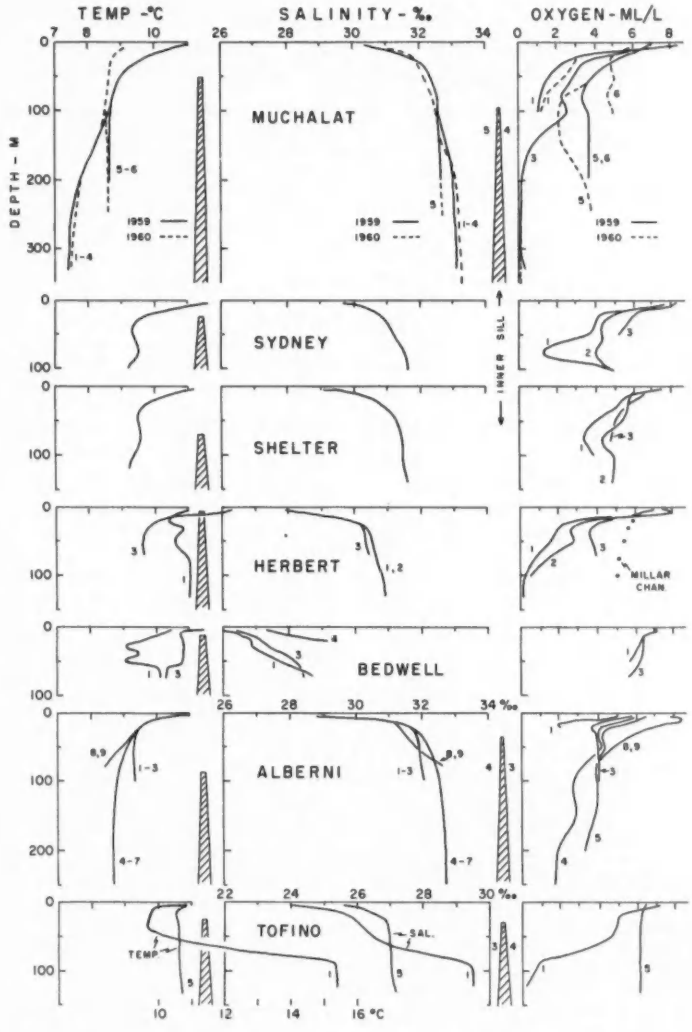


FIG. 7. Characteristic vertical profiles of temperature, salinity and dissolved oxygen for southern inlets in Vancouver Island from Muchalat to Alberni.

TABLE III. Mean values of salinity (‰) along the length of each inlet for each cruise, with range of salinity above mean which includes at least 75% of all values for each cruise (1959 to 1961 data, University of British Columbia).

Inlet	Date	Depth					Notes
		10 m	20 m	50 m	100 m	200 m	
Holberg	May 59	29.9±0.2	30.2±0.2	30.8	31.0		1
Neroutsos	May 59	30.8±0.3	31.8±0.6	32.8±0.1	33.1±0.2	33.3±0.2	
Tahsish	May 59	31.5±0.2	32.2±0.1	32.6±0.1	32.7±0.1	33.1	
Zeballos	May 59	30.8±0.2	31.3±0.2	31.6	31.9	32.1	
Tahsis	May 59	30.8±0.2	31.3±0.2	32.1±0.2	32.1±0.1		
					32.6		2
Tlupana	June 60	31.0±0.3	31.7	32.3	32.6	33.0	
Muchalat	May 59	30.9±0.1	31.4±0.1	32.3±0.2	32.6±0.1	33.0	3
						32.7	4
					(300 m 33.1)		5
	June 60	31.0±0.2	31.8±0.2	32.1±0.1	32.5	33.1	3
						32.6	4
					(300 m 33.2)		5
Sydney	May 59	30.0±0.3	30.8±0.3	31.2	31.2		
Shelter	May 59	30.0±0.3	30.6±0.1	31.3	31.4		
Herbert	May 59	28.8	29.4±0.4	30.4±0.2	30.8		
Bedwell	May 59	27.1±0.6	27.1±0.2	28.0±0.3			
	Mar. 60	26.9	27.4	27.6			6
	June 60	25.9±0.1	26.3	27.2			6
	Feb. 61	22.3	24.5	26.0			6
	Aug. 61	29.4	29.5	29.9			6
Tofino	May 59	25.0±0.2	25.8±0.2	26.4	29.5		7
		26.3	26.5±0.1	27.0	27.0		8
	Mar. 60	25.3±0.1	26.1±0.1	26.9±0.2	28.7		7
		26.1±0.1	26.6	27.0	27.0		8
	June 60	24.3±0.2	25.1±0.1	26.3±0.2	28.9		7
		25.4	25.8±0.1	26.3	26.5		8
	Sep. 60	28.2±0.2	28.6±0.1	28.9	28.9		7
		29.0	29.0	29.3			8
	Dec. 60	25.7±0.2	26.3±0.2	27.2±0.6	28.7		7
	Feb. 61	21.5±0.3	23.2±0.2	26.5±0.5	28.7		7
		23.3±0.3	24.0±0.2	24.4±0.1	24.8		8
	Apr. 61	22.7±0.1	23.4±0.2	25.6±0.3	28.8		7
		23.8	24.2	24.5			8
	Aug. 61	27.9±0.1	28.2±0.1	28.3±0.3	—		7, 9
		28.8	29.0±0.2	29.4	29.5		8, 9
	Aug. 61	28.3±0.1	28.7±0.1	28.9±0.1	28.9		7, 10
Alberni	May 59	30.7±0.4	31.5±0.2	31.9±0.1	32.2		11
				32.0±0.2	32.5	32.7	12

Notes:

1. When the ± range including at least 75% of the values at a particular depth was 0.07‰ or less it has been omitted.
2. At Sta. TAH 6; 57 m depth sill between this and TAH 1–3.
3. MUC 2–4 at 200 m.
4. MUC 5 at 200 m.
5. MUC 2 and 3 at 300 m.
6. BED 3 only.
7. TOF 1–3.
8. TOF 4 and 5.
9. August 15/16, 1961.
10. August 30/31, 1961.
11. All stations to 20 m, ALB 1–3 at 50, 100 m.
12. ALB 4–9 for 50, 100, 200 m.

A summary of the numerical values of salinity and temperature is contained in Tables III and IV. In these Tables, mean values are for the length of an inlet or of a basin, with an indication of the variability expressed as the '75% range'. This is a range either side of the mean which includes at least 75% of the values at the particular depth. The mean values of temperature and salinity are also summarized graphically in the temperature–salinity plots of Fig. 9. It should be noted that additional sources of data for some of these inlets are referred to in the Introduction.

TABLE IV. Mean values of temperature (°C) along the length of each inlet for each cruise, with range of temperature about mean which includes at least 75% of all values for that cruise (1959 to 1961 data, University of British Columbia).

Inlet	Date	Depth					Notes
		10 m	20 m	50 m	100 m	200 m	
Holberg	May 59	9.5±0.6	8.9±0.1	9.1±0.1	9.1±0.1		1
Neroutsos	May 59	9.0±0.3	8.7±0.3	7.9±0.2	7.5±0.4	7.4±0.2	
Tahsish	May 59	10.0±0.3	9.2±0.2	8.6±0.2	8.3±0.1	7.8±0.1	
Zeballos	May 59	10.1±0.2	9.5±0.2	9.2±0.1	9.4±0.2	9.3±0.2	
Tahsis	May 59	10.1±0.4	9.6±0.2	9.0±0.2	9.1±0.1		
					8.6		2
Tlupana	June 60	8.9±0.3	8.7	8.6	8.5	8.2	
Muchalat	May 59	10.5±0.3	9.8±0.2	8.9±0.2	8.7±0.2	7.8	3
						8.6	4
					(300 m 7.4)		5
	June 60	9.0±0.5	9.0±0.3	8.8±0.2	8.7±0.3	7.9	3
						8.6	4
					(300 m 7.6)		5
Sydney	May 59	10.8±0.5	10.0±0.4	9.4±0.4	9.2		
Shelter	May 59	10.3±0.5	10.0±0.5	9.5	9.4		
Herbert	May 59	11.2±0.8	10.1±0.4	10.1±0.5	11.0±0.1		
Bedwell	May 59	10.6±0.5	10.3±0.6	10.3±0.6			
	Mar. 60	7.4	7.4	7.4			6
	June 60	11.6±0.2	11.4±0.1	11.0±0.4			6
	Feb. 61	7.9	8.4	8.6			6
	Aug. 61	14.3	14.2	13.9			6
Tofino	May 59	10.3±0.4	9.8±0.5	9.9±0.3	15.4		7
		10.6	10.6	10.6	10.6		8
	Mar. 60	8.0±0.2	8.3±0.7	9.9±0.7	13.3		7
		7.3±0.2	7.3±0.1	7.2	7.2		8
	June 60	10.4±0.6	9.2±0.5	9.1±0.2	13.9		7
		11.1±0.2	11.0±0.3	11.0±0.1	10.9		8
	Sep. 60	13.4±0.2	13.2±0.1	13.5	13.5		7
		13.4	13.4	13.3			8
	Dec. 60	12.5±0.6	12.2±0.6	12.6±1.0	13.4		7
	Feb. 61	8.6±0.3	9.0±0.3	11.6±0.3	13.5		7
		8.4±0.1	8.4	8.4	8.5		8
	Apr. 61	9.0±0.3	9.0±0.3	10.5±0.3	13.4		7
		8.9	8.9	8.9			8
	Aug. 61	13.6±0.2	14.0	14.2±0.2	14.3		7, 9
		14.7	14.2±0.2	14.3	14.3		8, 9
	Aug. 61	14.5±0.3	14.5±0.2	14.6±0.3	14.6		7, 10
Alberni	May 59	9.8±0.2	9.5±0.2	9.37	9.3		11
				9.0±0.2	8.8±0.2	8.6±0.2	12

Notes:
1. When the ± range including at least 75% of the values at a particular depth was 0.07C° or less it has been omitted and the mean temperature quoted to the nearest 0.1C°.
2. to 12. As for Table III.

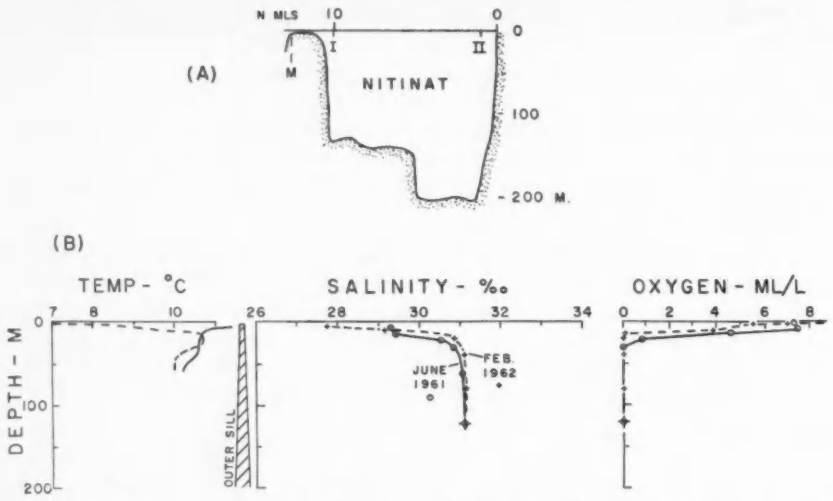


FIG. 8. Nitinat Lake; (A) longitudinal section, (B) vertical profiles of temperature, salinity and dissolved oxygen. (Data from T. G. Northcote.)

In the Vancouver Island inlets, as in the mainland ones, the greater part of the salinity and temperature change in the vertical column takes place in a few tens of metres just below the water surface. This part of the vertical column will be referred to as the 'upper zone'.

In the next two sub-sections attention will be drawn to features of the 1959 and 1960 property distributions, while in the Discussion some attempt will be made to account for some of the features.

3.21 SALINITY–DEPTH PROFILES

Below the surface the salinity increased as the depth increased in almost all cases, but the variation with depth was not the same in all inlets nor at all stations along an inlet. In Fig. 10 are shown the two basic types of salinity–depth profile in the upper zone, three variations of Type 1 being recognized.

In the localities where the surface salinity was much less than the deep water value the Type 1b profile was most common. In this there was a low-salinity surface layer of one or two metres depth in which the salinity increased slowly with depth. Below this the salinity increased rapidly over a limited depth range (the halocline zone) and thereafter increased only slowly with depth. The surface layer and halocline zone together formed the upper zone and occupied only a part of the inlet depth. In some cases the surface salinity was only a few parts per thousand, the surface layer was almost homogeneous, and the halocline started abruptly (Type 1a profile). This type of profile was characteristic of the head of an inlet near one of the larger rivers. In the inlets in which there was a low-salinity surface layer, the salinity of this increased toward the mouth as a result of upward mixing of saline water (Tully, 1949) and the

halocline became less steep (Type 1c profile) (cf. Pickard, 1961, p. 934 for the mainland inlets and Herlinveaux, 1962, p. 15 for Saanich).

In other inlets there was no well-defined surface layer and the halocline started at the surface (Type 2 profile). This was characteristic of the inlets with small river runoff.

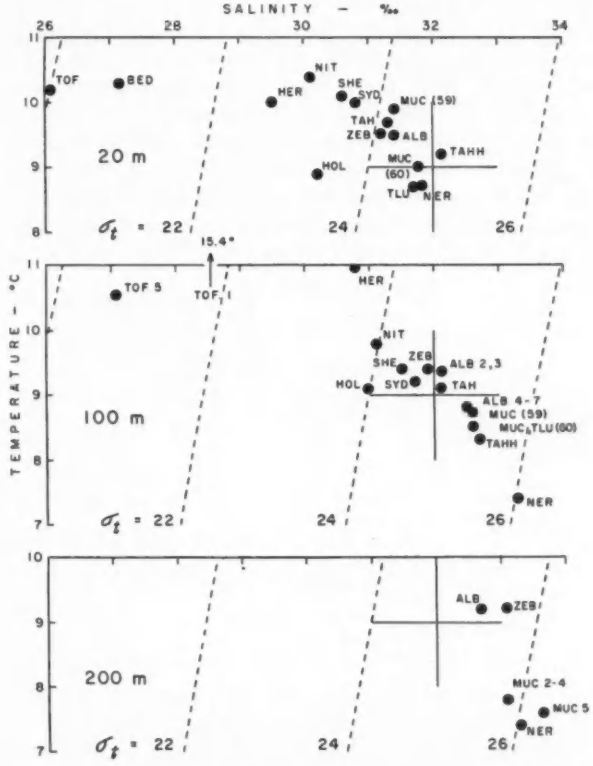


FIG. 9. Summary of mean temperature–salinity characteristics of the water at 20-, 100- and 200-m depth in Vancouver Island inlets.

It should be pointed out that Fig. 10 is intended to illustrate only the *shape* of the salinity–depth profile. The thickness of the surface layer and the steepness and thickness of the halocline varied from inlet to inlet and could only be stated for individual inlets. The type profiles shown in Fig. 10 represent the profile only to the bottom of the halocline and therefore cover only a part of the total inlet depth. Below the halocline the salinity changes were usually small compared to those in or above it.

The thickness recorded for the surface layer during the May–June period of the 1959 and 1960 cruises was usually 2 m or less and was too small to show

clearly in the profiles in Fig. 6 and 7. Table V has been prepared to supplement these figures by presenting numerical values for the surface and deep water salinities, the types of salinity–depth profile and the depths where the salinity reached 50, 90 and 95% of the deep-water value.

From Table V it will be seen that a salinity profile of Type 1a with a sharply defined surface layer was only observed in Alberni and in Muchalat (in 1959). In six inlets there was a less sharply defined surface layer with a Type 1b or 1c salinity profile at the head and in five the profile was of Type 2 with no clearly defined surface layer. Since the salinity measurements near the surface were made at 2-m intervals (the minimum practicable with the water sampling bottles used) the thickness quoted for the surface layer is to be taken as an upper limit. The layer thickness was also estimated from the depth of the thermocline on the bathythermogram obtained at each station, the assumption being made that the thermocline and halocline were coincident (as had been shown to be the case for the mainland coast inlets, Pickard, 1961, p. 936). The values of 0–8 m for the

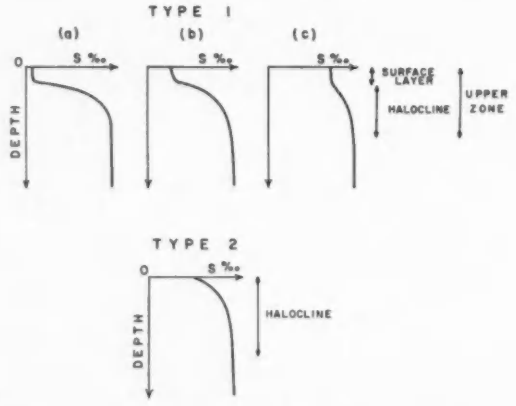


FIG. 10. Types of vertical profile of salinity in the upper zone in British Columbia inlets.

'90% depth' (excepting Tofino) and of 0–20 m for the '95% depth' (excepting Tofino and Bedwell) are the basis for the statement made earlier that the surface layer and halocline zone together occupied only a small part of the total inlet depth. Both the surface layer thickness and the halocline depth were generally less in the Vancouver Island inlets than in the mainland coast inlets (Pickard, 1961, p. 935).

In Tofino at Sta. 1 the water structure was unusual. In addition to the normal shallow halocline zone at 5–10 m there was a deep halocline zone from 50 to 90 m (Fig. 7). In Bedwell, adjoining Tofino, a similar double halocline was observed at Sta. 1, the deeper halocline extending to the bottom at 75 m.

TABLE V. Surface and deep salinity values and salinity profile characteristics in inlets along the west coast of Vancouver Island (May 1959 and June 1960 data).

Inlet	Salinity (‰)						Salinity–depth profile						
	Surface		Deep	Type[2]			Depth of surface layer near inlet head	Dimensions[3] 50% depth		90% depth		95% depth	
	Mo	Hd		Mo	Mi	Hd[1]		Mo	Hd	Mo	Hd	Mo	Hd
							m	*m*	*m*	*m*	*m*	*m*	*m*
Holberg	23	28.5	31.0	1c	1c	2	0	0	0	2	0	10	0
Rupert	28.5	28.5	31.0	1c	–	1c	2	0	0	0	0	0	5
Neroutsos	31.5	8	33.3	2	1c	1b	1 to 2	0	2	0	5	4	14
Tahsish	30.5	16	33.1	1c	1c	1b	1 to 2	0	0	0	6	13	9
Zeballos	30.5	25	32.1	1c	1c	1b	2	0	0	0	4	2	7
Tahsis	28	13	32.1	1c	2	2	0	0	0	7	3	10	7
Tlupana 1960	18.5	9.5	33.0	2	2	2	0	0	2	5	4	13	10
Muchalat 1959	22	3	33.1	2	2	1a	2	0	2	3	3	15	20
1960	24	3.5	33.2	2	2	1b	2	0	2	6	7	12	16
Sydney	29	25	31.2	1c	1c	1b	2	0	0	0	6	12	11
Shelter	28	26.5	31.4	1c	2	2	0	0	0	3	2	7	11
Herbert	27.5	20	30.8	1c	1b	2	0	0	0	3	4	12	14
Bedwell	27	12	28.0	1c	1c	1b	1 to 2	0	2	0	4	15	40
Tofino 1959	21	7	29.5	1c	1c	1b	1 to 2	0	0	0	0	0	5
1960	28.5	4	28.9	2	–	1b	3	–	2	25	50	17	100
Alberni	28.5	1.5	32.7	1c	1b	1a	5	0	5	8	6	13	10

Notes:

1. Mo = Mouth, Mi = Middle, Hd = Head of inlet.
2. For explanation of salinity profile types see Fig. 10 and text, Section 3.21.
3. Depths in metres at which the salinity reaches 50, 90, and 95% respectively of the maximum salinity in that inlet.

3.22 TEMPERATURE–DEPTH PROFILES

Table IV was prepared from reversing thermometer observations at the depths quoted and gives a broad description of the temperature structure. The use of a bathythermograph at each station yielded details of the temperature structure such as are not available for salinity and which may not be apparent in Table IV, although some are apparent in Fig. 6 and 7. Some of the details are described below.

The temperature generally decreased as depth below the surface increased, with an increase in temperature gradient (thermocline) in the region of the halocline. Generally the temperature decreased by 2 to 6 C° between the surface and a depth of 10–12 m in the inlets from Alberni to Tahsis. In the northern inlets from Zeballos to Neroutsos the temperature decreased by 4 to 7 C° between the surface and 30 m except at Sta. 7 to 9 in Neroutsos where the thermocline continued to about 100 m. The chief exceptions to the above generalizations were in Tofino, at Sta. 4 and 5, and Holberg, where the temperature decrease was only 1 C° to 10 m depth.

Below the thermocline the rate of decrease of temperature was less, usually 0.5–1.5 C° to the bottom of the inlet at 100–300 m, as may be seen in Table IV. There were some exceptions to this. The most remarkable was in the Tofino basin where at Sta. 1 in 1959 the water temperature reached a minimum value of 9.6 °C at about 30 m and then *increased* by 5.8 C° to 85 m depth, below which it became isothermal at 15.4°C to the bottom at 125 m. The shallower Sta. 2 and 3 were consistent with Sta. 1, but at Sta. 4 and 5, in the Fortune basin, the water was isothermal within 0.2 C° from 10 m to the bottom at 140 m. The temperature structure in Bedwell showed some similarity to that in Tofino, with a decrease from the surface and an increase of 1.3 C° from 50 to 65 m. The deep water temperature–salinity characteristics in Tofino and Bedwell are similar to those of the surface water in the Pacific Ocean outside the inlets in the summer but the mechanism for its introduction to the inner basins of the inlets is not known.

In Muchalat the water in the outer basin was nearly isothermal from 70 to 200 m but in the inner basin the temperature continued to decrease to 250 m and was uniform from there to the bottom at 350 m. In Holberg the temperature was uniform to within ±0.1 C° from 20 m to the bottom at 110 m.

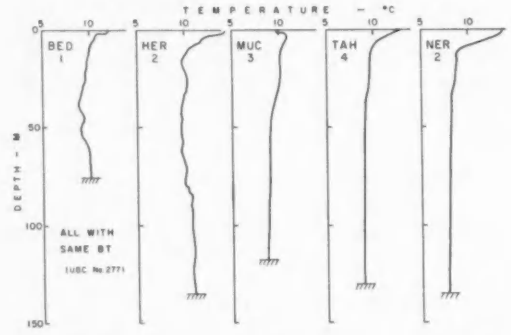


FIG. 11. Examples of bathythermograph traces in Vancouver Island inlets to contrast the fine structure evident in some southern inlets with the smoother profile in most inlets.

A feature in some inlets was the fine structure (series of small maxima and minima) visible on the bathythermograms. Two such vertical temperature profiles are compared in Fig. 11 with examples of the more common smooth trace. The inlets showing the fine structure feature at some or all stations were Bedwell, Herbert, Sydney and Tahsis. It is presumed that this resulted from periodic inflows of ocean water, the water settling at a level determined by its density in relation to the density structure of the water already present. Since the density is determined chiefly by salinity in these waters it is presumed that the small inversions of temperature are balanced by sufficient increases in salinity to maintain an increase of density with depth so that the water is stable.

In addition to that described for Tofino and Bedwell there was a distinct mid-depth temperature minimum in a few inlets, e.g. in Shelter and Sydney at 50 m, Tahsis at 50–100 m and Zeballos at 40–70 m.

4. DISSOLVED OXYGEN

In describing the water properties of the mainland coast inlets (Pickard, 1961) it was stated to be more difficult to summarize the data on dissolved oxygen distributions than on temperature and salinity. This proved to be the case for the Vancouver Island inlets as well. There are two main reasons for this. The first is a consequence of the fact that natural water bodies are stratified horizontally, or nearly so, with respect to density. Since density is determined in these inlet waters by salinity, and to some extent by temperature, these two properties usually have horizontal stratification and consequently have limited variations in the horizontal direction, their main changes being in the vertical direction only. However, the dissolved oxygen content has no significant effect on the density and therefore oxygen distributions without horizontal stratification are quite possible and, in fact, quite common. The second reason is that while the factors which may alter the salt or heat content of a natural water body act at the upper surface only, there may be production and consumption of oxygen below the surface, e.g. photosynthetic production in the upper layers, and consumption by living organisms, pollutants or detritus at any depth. Since the sources or consumers of dissolved oxygen may have marked horizontal variations it is possible for the oxygen content to exhibit marked horizontal variations in addition to vertical ones.

It was not practical to summarize the oxygen distributions in the inlets of the west coast of Vancouver Island in groups as was done for the mainland inlets. Instead, typical vertical profiles are presented graphically in Fig. 6, 7 and 8B. Only sufficient profiles are shown to illustrate the range of variation in each inlet.

In Alberni the oxygen distribution was similar to that described by Tully (1949, p. 66) with low values toward the inlet head and a distinct minimum at 15–25 m at Sta. 1 to 4. A curious feature was the low oxygen content below 50 m at Sta. 4 with higher values on either side. A somewhat similar situation was evident in the June 1941 survey described by Tully (1949, p. 65) and in the September 1954 observations by Waldichuk (1956, p. 12). The high values in Imperial Eagle Channel (Alberni Sta. 8 and 9) may be attributable to photosynthesis (cf. Tully, 1949, p. 66), although the upper waters were more transparent (Secchi disc depth of 6.5 m) than is usually the case when there is abundant phytoplankton present.

In the Tofino basin (e.g. Sta. 1) in 1959 the oxygen content decreased sharply in the deep halocline to low values in the bottom water, while in the Fortune basin (e.g. Sta. 5) the water was almost uniform in oxygen content from top to bottom. In 1960 the Tofino basin showed further depletion of oxygen below the depths of the sills separating Sta. 1 and 1/2 and 0, with zero values at the bottoms of these small inner basins (Anon., 1960b).

Bedwell had relatively well-oxygenated water (of low salinity) to its maximum depth of 70 m but in Herbert, next to it, there was a sharp decrease from 10 to 30 m and a less rapid decrease below this, with a value of 0.2 ml/l below 100 m at Sta. 1.

The next inlet to the north (Shelter) had a minimum at 75 m but the value of 3.4 ml/l was higher than that in Herbert. The difference between these neighbouring inlets may be due to the sill depth for Shelter (24 m) being greater than that for Herbert (8 m). At the same time it is noted that at the north end of Millar Channel the oxygen values to 100 m depth were much higher than in Herbert and as high as or higher than those in Shelter. Millar connects at its south end with Herbert (and its 8 m sill to the Pacific) and at the north end with Shelter by Hayden Passage which is only 35 m deep. The lower values in Sydney, Sta. 1 and 2, for 75 m may again be associated with the shallow sill depth (24 m).

In the connecting inlets, Muchalat, Tlupana and Tahsis, there were similar oxygen distributions. In Muchalat, between 10 and 90 m, there was a progressive decrease in dissolved oxygen from the mouth (Sta. 6) to the head (Sta. 1). In the inner basin (Sta. 1 to 4) the low values for dissolved oxygen suggest that the circulation is slight. In 1960 the water below 150 m had not changed significantly from 1959 in the inner basin but there were marked changes in the outer basin at Sta. 5 and 6, nearer to the ocean. Lower values were found in the inner basin of Tahsis particularly toward the inlet head above Tsowwin Narrows. Tlupana also had low values toward the inlet head in the deep water although the sill between it and Tahsis–Muchalat is deep.

In Zeballos a mid-depth oxygen minimum was observed. The rise in oxygen content below 150 m together with a decrease in temperature and rise in salinity below 150 m suggest that the deep water had recently entered the inlet or possibly that a continuous slow inflow occurs.

In Tahsish, the oxygen content had a minimum between 20 and 75 m with values decreasing toward the head. The very marked change between Sta. 1 and 2 occurred well above the sill between these two stations. The high oxygen values between 100 m and the bottom at Sta. 2 to 4 suggest that this deeper water had recently entered the basin. It is possible that the state observed was a dynamic one with the water actually penetrating at the time of observation. That this may have been the case is suggested by small discontinuities in the temperature structure as revealed by bathythermograms (not shown) from 55 to 70 m at Sta. 4 and 3, and from 75 to 80 m at Sta. 2. At Sta. 1 a small discontinuity was evident at 120 m on the bathythermogram but as the deepest water sampling bottle was at 100 m there is no confirmation from salinity or oxygen values that the possible inflow of water had reached this position.

The unusual condition in Neroutsos of very low oxygen values near the surface has been described previously (Waldichuk, 1958) and is attributed by him to the oxygen demand of the effluent from the sulphite pulp mill at Port Alice between Sta. 1 and 2 (Fig. 2). Below the surface there was in 1959 a maximum at 6 m, a minimum at 20 to 30 m, and an increase below this at Sta.

1 to 3. In the deeper water, below 50 m, the oxygen values showed only a small decrease with depth and showed only small changes along the inlet, being higher in the inner basin (Sta. 3 and 4) than outside (Sta. 7 to 9). Dr M. Waldichuk (private communication) has suggested that this latter condition might be the result of replacement of the deep water in the outer basins by upwelled, low-oxygen content, Pacific Ocean water at this time of the year. This possibility is considered further in the Discussion.

In Holberg and Rupert it had been anticipated that the shallow sill of Quatsino Narrows separating them from Neroutsos would result in stagnation and low dissolved oxygen values. It will be seen from Fig. 6 that this was not the case. In fact, apart from the deepest sample at the head of Holberg, the water in the two inlets was remarkably uniform from top to bottom with the highest oxygen values at 100 m of all Vancouver Island inlets except Sydney and in Millar Channel.

In Nitinat the rapid decrease in dissolved oxygen to zero values at and below 20–30 m will be noted.

5. WATER TRANSPARENCY IN THE SURFACE LAYER

The Secchi disc depth was measured at each station. The mean value for each inlet increased from south to north from 4 m in Alberni to 9 m in the outer (Quatsino) section of Neroutsos, with individual values lying within ±1–2 m of the mean. In the inner part of Neroutsos (Sta. 1 to 4) the mean was 2.5 m. These values for Neroutsos may be compared with those measured in 1957 by Waldichuk (1958) of 7 m in Quatsino and of 2–5 m in Neroutsos proper. In Holberg the mean was 12 m with a range from 15.5 at the head (Sta. 1) to 6 m near Quatsino Narrows.

In Neroutsos both the reddish-brown colour of the surface water toward the inlet head and foam on the surface as described by Waldichuk (1958) were noted in 1959.

6. DISCUSSION

6.1 Temperature–Salinity Characteristics

On the basis of the temperature–salinity plots for the subsurface waters (Fig. 9) the Vancouver Island inlets may be divided into two groups. The Clayoquot Sound group (Tofino, Bedwell and Herbert) has higher temperatures, lower salinities and larger ranges of salinity than the remainder. At each depth, the properties for the remaining inlets, i.e. the majority, lie within an area on the temperature–salinity plot of about 2 C° by 2‰ in dimensions. For the Clayoquot Sound group the mean values are about 1.5 C° higher in temperature and 4‰ lower in salinity than for the remainder.

6.2 Source of Deep Water and Effect of Outer Sill Depth

A characteristic of the Clayoquot Sound group is that it has the shallowest sills of the inlets along the Vancouver Island coast for which oceanographic data was obtained in this survey. This suggested a possible reason for the difference

in water properties between this group and the remainder, and further suggested examining the correlation between the deep water properties and the sill depths for all the inlets. The results of this examination indicate that, with a few exceptions, the subsurface water characteristics have a systematic relationship to the outer sill depth as illustrated in Fig. 12. In this Figure are plotted the mean temperature (Fig. 12A) and salinity (Fig. 12B) of the water for each inlet (from Tables IV, III, VIA and Tully, 1937, at 50, 100 and 200 m depth against the effective sill depth (see Section 2.1) of that inlet. Values for 50 m are given only for those inlets with sill depths much less than 50 m. In the case of inlets with more than one basin, the data for the outer basin have been used. The full lines represent envelopes of the temperature and salinity points. Although there is considerable scatter, the envelopes on each plot show a systematic

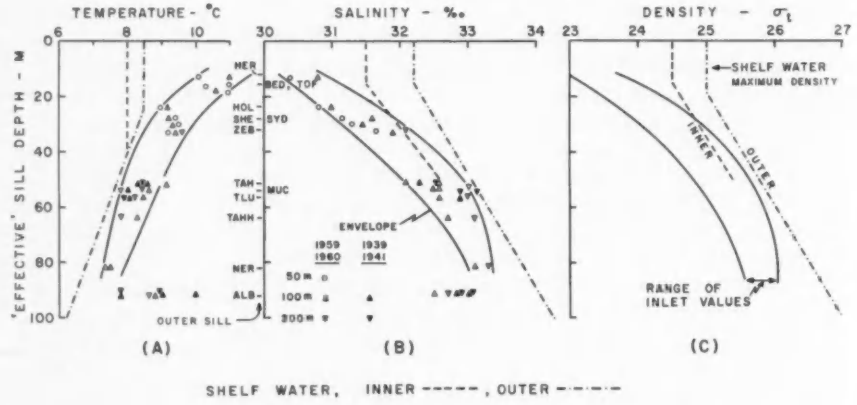


FIG. 12. Temperature and salinity in Vancouver Island inlets at 50, 100 and 200 m, where these depths are below the sill depth, against sill depth, together with profiles of temperature, salinity and density (σ_t) for ocean water outside the inlets during the period of maximum density of the ocean water.

decrease of temperature and increase of salinity with increase in sill depth. Fig. 12C shows the range of density (σ_t) versus sill depth corresponding to these envelopes (i.e. to the maximum temperature with the minimum salinity and to the minimum temperature with the maximum salinity). In other words it shows the range of densities which may be found in the deeper waters of the inlets. It should be noted that 90% of the variation with depth of density is due to the variation with depth of salinity and only 10% to the variation of temperature.

It is interesting to compare these subsurface water characteristics inside the inlets with the source waters in the Pacific Ocean over the continental shelf off the west coast of Vancouver Island. The ocean waters show very marked seasonal variations in temperature and salinity both at the surface (Pickard and McLeod, 1953) and below the surface (Lane, 1962).

The character of the surface salinity and temperature variations is shown in Fig. 13 from data of the Pacific Oceanographic Group (Anon., 1953; Hollister, 1960). These surface waters are less saline and less dense than the waters in the inlets at 20 m or more depth, except in the Clayoquot Sound group (Section 6.1). Since the stations (Kains, Nootka and Amphitrite) for which the surface water characteristics are shown in Fig. 13 are at the mouths of inlets, the low salinity of the surface water is presumably evidence of the estuarine circulation in the

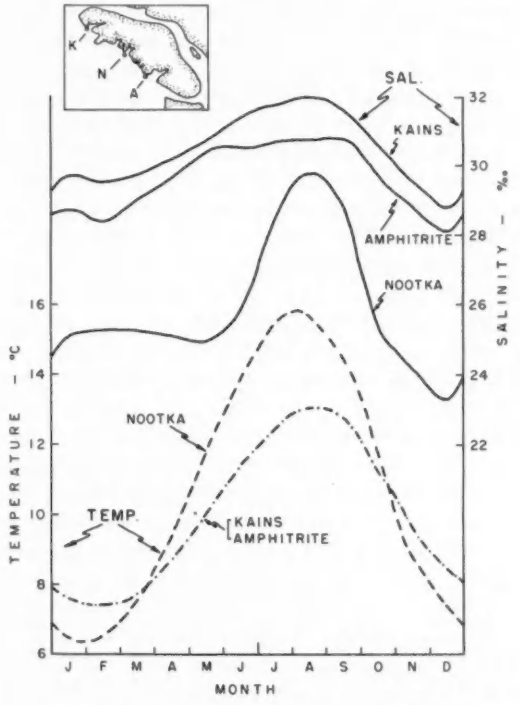


FIG. 13. Monthly mean values of salinity and temperature of the surface water at light stations along the Vancouver Island coast. (Nootka from 1935 to 1952, Kains and Amphitrite from 1950 to 1959.)

inlets with the surface layer having a net motion to seaward throughout the year. The source of the deep water in the inlets must therefore be in the subsurface water of the Pacific Ocean.

Since the surface outflow from the inlets includes saline water entrained from below within the inlets some inflow of subsurface water must continue throughout the year as a component of the estuarine circulation driven by the river runoff. This runoff appears to be small in most of the Vancouver Island inlets and the estuarine inflow is probably much less than that into the mainland inlets which

have larger rivers in many cases. It is therefore presumed that inflow of subsurface water over the sills to the inlet basins takes place chiefly when the density of the outside water column is at its seasonal maximum at and above sill depth. The dashed lines in Fig. 12C represent the average variation with depth (using the sill depth scale) of the maximum density in the annual cycle in Pacific Ocean waters at two stations off the west coast of Vancouver Island during 1959 to 1961. These curves are taken from studies made by Lane (1962, and unpublished reports) of data collected by the Fisheries Research Board of Canada, Pacific Oceanographic Group. The inner station is 5 miles southwest and the outer is 20 miles southwest of Amphitrite Point (Fig. 1). On the temperature and salinity plots the dashed lines represent the minimum temperature and maximum salinity at these stations. The maximum densities for the outside waters occur during August to October for the outer station, and during October to December for the inner station. It is seen that the density of the waters in the inlets is always less than the maximum value outside for the 1959–61 shelf data, while the inlet temperature values are greater than the outside minima and the salinities less than the outside maxima.

It is suggested that the above facts indicate that the maximum values for the density of the shelf waters observed by the Fisheries Research Board of Canada (Pacific Oceanographic Group) in 1959–61 are probably typical of long term conditions. This suggestion is based on the fact that the temperature and salinity values from the inlets plotted in Fig. 12 are for 100 and 200 m which are below the maximum sill depths of any of the inlets, and on the assumption that the waters in these basins will be displaced only when more dense water occurs above sill depth outside the sills than within. If this is the case the inlet waters act as a "memory" of maximum density conditions outside. The higher temperature and lower salinity of the inlet waters than the extreme values outside may be indicative of the spread of values or of small differences in the shelf waters along the coast, or may be due to downward diffusion of heat and of fresh water within the inlets. The latter may certainly be expected to occur as suggested by Tully (1949). A similar situation was observed in the mainland inlets in side basins separated from the main basins by relatively shallow sills (Pickard, 1961). The inlets in Vancouver Island which have the shallowest sills show the greatest differences from the outside water characteristics. These differences are greater than appear in Fig. 12A and 12B because some high temperature and low salinity values for Tofino and Bedwell are beyond the limits of the graphs presented there. (The reader is reminded that the points plotted in Fig. 12A and 12B, and the full line envelopes, are for the deep water at 50, 100 and 200 m depth in the inlets, the depth scales in this case being for the sill depth of the inlet. The dashed lines however represent depth profiles of the respective properties outside the inlets.)

In discussing the deep zone water characteristics for Alberni, Tully (1949, p. 73) stated "Under these circumstances it would be expected that the deep-zone waters would reach a limiting density in some year of extreme upwelling and would thereafter be permanent." Later he stated "Consequently during the

winter there would be a slow exchange of water between the middle and deep zones so that the density of the latter would become less; then with the advent of summer the conditions for direct displacement by upwelling ocean water would be restored." If these were offered as alternative hypotheses, contrasting (a) the possibility of infrequent replacement of the deep water with (b) that of replacement every year, the present writer would support the latter on the basis of the observations now available for the majority of the larger inlets of Vancouver Island.

The reason for the points for Alberni falling off the general trend of the curves is not known. It is possible that the considerable length of the shallow entrance through Imperial Eagle Channel results in some vertical mixing so that the deep water which eventually passes through Junction Passage (Fig. 3) into the main basin of Alberni has had its salinity decreased and temperature increased by mixing with the upper waters.

6.3 Periodic Changes

There are no time series of observations sufficient to permit an adequate description of the seasonal variations of properties, with the possible exception of some data for Tofino (Anon., 1959, 1960b, 1961). These observations indicate that Tofino is flushed at intervals but there is some question about the mechanism as there are two entrances from the ocean to this inlet.

For Alberni there are the data obtained by Tully for 1939 and 1941 in his classic study (Tully, 1949; Anon., 1957), by Waldichuk for 1954, 1957, 1959 and 1961 (Waldichuk, 1962) and the present data by Pickard for 1959. There are also some data for the Nootka Sound inlets (Tully, 1937) and for Neroutsos (Hutchinson and Lucas, 1927; Waldichuk, 1958) in addition to the data described in the present paper.

6.31 Alberni Inlet

For Alberni there are some data for six years between 1939 and 1961 and typical values are presented in Tables VIA and VIB. The first of these contains data representative of the main or outer basin of the inlet while the second shows data for the shallower inner basin. The data for 1939 are the means for stations occupied on October 31 and November 1. For 1941, Sta. B and C were occupied 15 times in May, June and July. At some depths there is a marked difference between the data for the seven stations from May 22 to June 7 and those for the eight stations from June 23 to July 4. Mean values are given in Tables VIA and VIB for each of these two periods which will be referred to as 'May–June' and 'June–July'. The 50 m values tabulated for 1941 are the means of Tully's observed values at 40 and 60 m. The data in Tables VIA and VIB for September 1954 and for August 1957 are interpolations at the tabulated depths by the present author from Waldichuk's original data.

Although these data are insufficient for a full description of the seasonal variations of properties they do give some indication of the magnitude of the variations in values which occur in this inlet, and they also give information about the inflow of water from the outside. The range of values for each of the water

TABLE VIA. Typical values for the outer basin of Alberni Inlet of salinity, temperature and dissolved oxygen for the period 1939 to 1961 with the range of values (i.e. maximum minus minimum). Values for May/June 1941 and for June/July 1941 are mean values for several cruises during each of these periods. Stas. 3, C and A6 are all close to U.B.C. Sta. 4 (Fig. 1).

Depth (m)	Tully Sta. 3	Tully Sta. C		Waldichuk Sta. C	Waldichuk Sta. A6	Pickard Sta. 4	Waldichuk Sta. A6		Range: maximum minus minimum
	Nov. 1939	May/ June 1941	June/ July 1941	Sept. 1954	Aug. 1957	May 1959	Aug. 1959	Oct. 1961	
Salinity (‰)									
10	31.66	31.17	31.47	31.4	31.25	30.34	31.44	31.73	1.4
20	31.82	31.62	31.84	31.6	31.55	31.46	31.91	32.00	0.5
50	32.35	32.37	32.48	31.9	32.05	32.22	32.66	32.62	0.8
100	33.04	32.62	32.75	32.7	32.6	32.56	32.90	32.98	0.5
150	33.05	32.73	32.81	–	–	32.61	32.94	33.02	0.4
200	33.10	32.77	32.84	–	–	32.67	32.97	33.05	0.4
250	–	–	–	32.8	32.8	32.68	32.98	–	0.3
Temperature (°C)									
10	10.24	11.43	11.85	10.6	11.1	9.83	10.62	10.53	2.0
20	10.08	10.57	10.94	10.2	9.65	9.45	9.60	9.80	1.5
50	9.22	10.36	10.03	9.3	8.2	9.15	8.54	8.49	2.2
100	7.78	10.00	9.12	7.8	7.85	8.91	8.23	7.95	2.2
150	7.76	9.06	8.94	–	–	8.82	8.08	7.96	1.3
200	7.77	8.78	8.86	–	–	8.81	8.2	–	1.1
250	–	–	–	–	7.9	8.78	8.2	–	0.9
Oxygen (ml/l)									
10	3.79	5.83	6.92	5.05	5.5	5.62	4.60	3.78	3.1
20	3.00	4.11	4.60	4.25	4.15	4.11	3.55	3.00	1.6
50	2.12	4.06	3.38	3.0	2.9	4.25	2.48	1.84	2.4
100	0.65	3.49	2.06	2.15	1.85	2.72	1.94	2.09	2.8
150	0.96	1.82	1.98	–	–	2.86	1.85	1.96	1.9
200	0.82	1.31	1.73	–	–	1.89	1.80	1.48	1.1
250	–	–	–	1.7	2.05	1.78	1.78	–	0.4

properties is expressed in the form of the difference between the maximum and the minimum value at each depth and is given in the last column in each Table. The ranges may be summarized briefly as:

Range of	*Salinity*	*Temperature*	*Oxygen*
at 10 – 100 m is less than	1.4‰	2 C°	3 ml/l
at 150 m or deeper is less than	0.4‰	1.3 C°	2 ml/l.

From Tully's 1941 data over the period from May 22 to July 4 it is concluded that significant variations can take place in short intervals even in the deep water.

The changes in properties at some depths between the May–June and the June–July periods suggest that an inflow of water took place between the two periods or possibly was taking place during the whole time of observation. Comparison of the data for the June–July period with that for the May–June period for the outer basin (Table VIA) suggests that:

water initially at 60 m was displaced up to 40 m,

water initially at 90–100 m was displaced up to 60 m,

water initially at 140–150 m was displaced up to 100 m, and

water initially at 150–200 m was mixed with inflowing water of temperature greater than 8.9°C, salinity greater than 32.8‰ and oxygen content greater than 2.5 ml/l.

At Sta. B in the inner basin, separated from the outer basin by a sill of 36 m depth, there was no significant change of temperature or oxygen content between the May–June period and the June–July period (Table VIB) but there was a marked increase in salinity of 0.3‰. At first sight these facts appear inconsistent, but a closer comparison of the inner and outer waters indicates that this may not be so. In the June–July period the water from 40 to 100 m depth in the inner

TABLE VIB. Typical values for the inner basin of Alberni Inlet of salinity, temperature and dissolved oxygen for the period 1939 to 1961 with the range of values (i.e. maximum minus minimum). Values for May/June 1941 and for June/July 1941 are mean values for several cruises during each of these periods. Stas. 2, B and A7 are all close to U.B.C. Sta. 3 (Fig. 1).

Dep. (m)	Sta. 2	Tully Sta. B			Waldichuk Sta. B	Waldichuk Sta. A7	Pickard Sta. 3	Waldichuk Sta. A7		Range: Maximum minus minimum
	Nov. 1939	May/June 1941	June/July 1941	Aug. 1941	Sept. 1954	Aug. 1957	May 1959	Aug. 1959	Oct. 1961	
Salinity (‰)										
10	31.59	30.95	31.33	31.71	31.45	30.95	31.34	31.17	31.61	0.8
20	31.85	31.50	31.76	32.16	31.55	31.45	31.82	31.72	31.83	0.7
50	32.14	31.84	32.14	32.41	32.05	31.8	31.98	32.15	32.17	0.6
100	32.33	32.00	32.34	32.61	32.15	32.05	32.15	32.26	32.33	0.6
Temperature (°C)										
10	10.08	11.19	11.13	11.46	10.4	10.3	9.54	10.7	10.25	1.9
20	9.87	10.55	10.55	10.36	10.1	9.7	9.51	10.0	9.91	1.1
50	9.28	10.22	10.24	10.02	9.1	8.4	9.37	9.3	9.13	1.8
100	8.92	10.23	10.21	9.77	8.8	8.0	9.32	9.2	9.00	2.2
Oxygen (ml/l)										
10	3.03	5.27	5.60	4.22	4.65	4.7	4.41	4.08	3.12	2.6
20	2.46	3.76	3.86	2.48	3.95	4.15	3.68	3.62	2.98	1.7
50	1.80	3.27	3.25	2.25	2.45	3.05	3.95	3.14	2.14	2.2
100	1.18	3.42	3.40	2.22	1.7	3.85	4.00	2.95	2.18	2.8

basin had the same range of density (σ_t = 24.65 to 24.85) as that at 40–55 m depth in the outer basin during the May–June period. This outer basin water at 40–55 m was substantially isothermal at 10.3°C and had a salinity range from 32.1 to 32.4‰ while the water in the inner basin below 40 m in the later period was at 10.25°C and 32.5‰. These figures suggest that some of the water in the outer basin between 40 and 55 m when displaced upward by the presumed inflow of deeper water spilled over the 36 m sill into the inner basin. Being denser (σ_t = 24.65 to 24.85) than the deep water already there (σ_t = 24.45 to 24.6) it displaced some of it upward. One fact which is not quite consistent with this hypothesis is that in the later period the oxygen content in the inner basin was lower (3.3–3.5 ml/l) than that previously at 40–55 m in the outer basin (3.8–4.2 ml/l). A possible explanation is that the decrease in dissolved oxygen in the inner basin water in June–July was evidence of a seasonal increased oxygen demand associated with increased debris brought into the inlet by the rivers (Tully, 1949, p. 73). It is noted that the oxygen in the inner basin continued to decrease after June–July to a value of 2.9 ml/l by August 21.

A similar series of changes is evident between May and August 1959. In the outer basin there was an increase in salinity near the bottom by about 0.3‰ and in temperature by 0.8 C°. The data are consistent with an inflow of bottom water raising that previously (May) in the interval from 100 to 250 m to about the 50 m level by August. The oxygen values at 50 m depth in August are the same as those at 150–200 m in May, a change which is similar to that deduced to have occurred in 1941. However, in 1959 the values at 200 and 250 m are the same in May as in August indicating that the inflowing water had a very low oxygen content or possibly that the oxygen demand of bottom material stirred up by the inflowing water had reduced the latter's oxygen content.

In the inner basin in 1959 the changes in salinity and temperature of the deep water were again consistent with it having come over the 36 m sill from depths of the order of 50 m in the outer basin. Also, as in 1941, the oxygen content in August of the deep water in the inner basin was lower than that earlier at 50 m in the outer basin.

The evidence above for replacement of some, at least, of the deep water in Alberni in 1941 and in 1959, together with the fact that high salinities and low temperatures in the deep water are characteristic of the observations made in the later months in other years (Table VI A, 1939, 1957, 1961), suggests that the replacement takes place every year and not irregularly.

6.32 THE NOOTKA SOUND INLETS

Representative values of the water properties for Tahsis, Tlupana and Muchalat for 1933 obtained by Tully (1937) are compared in Table VII with the 1959 and 1960 values by presenting the differences between the later and the earlier values. The differences are larger in the upper zone as might be expected since the observations were not all made at the same time of the year and seasonal variations are greatest in the upper zone. (The 1933 values were obtained in late July, 1959 ones in late May and the 1960 ones in early June.) Since the

TABLE VII. Mean differences in some Vancouver Island inlets between recent (1959 or 1960) and earlier values for salinity (Δ S in ‰), temperature (Δ T in C°) and dissolved oxygen (Δ O_2 in ml/l) (+ indicates that the later value is the greater).

Depth (m)	Δ S	Δ T	Δ O_2	Δ S	Δ T	Δ O_2
	Tahsis (1959–1933)			*Tlupana* (1960–1933)		
10	−0.8	+0.8	+1.0	−0.9	−0.4	−2.2
20	−0.8	+1.0	+0.8	−0.6	+0.2	+0.1
30	−0.6	+0.9	+0.4	−0.5	+0.4	0
50	−0.3	+0.9	+0.2	−0.4	+0.4	−0.3
100	−0.3	+0.8	+0.2	−0.3	+0.5	−0.9
200	−0.2	+1.0	+0.2	0	+0.3	−2.4
	Muchalat (1959–1933)			*Muchalat* (1960–1959)		
10	−1.3	+1.6	+1.3	−0.1	−1.6	−1.5
20	−1.0	+1.3	+1.7	+0.4	−0.9	−0.5
30	−0.9	+0.8	+1.0	0	−0.6	0
50	−0.4	+0.8	+0.8	+0.1	−0.3	+0.5
100	−0.3	+0.7	+0.6	0	−0.1	−0.4
200	−0.2	−0.2	−0.4	+0.1	+0.1	−0.1
350	−0.1	−0.5	+0.1	+0.1	+0.2	−0.4
	Neroutsos (1959–1957)			*Neroutsos* (1959–1927)		
10	+0.1	−3.0	−1.7	−1.6	−2.8	+0.8
20	+0.8	−2.0	−1.3	−0.8	−1.9	+0.8
30	+1.1	−1.3	+0.4	–	–	–
50	+0.4	−0.3	+1.0	–	–	–
100	+0.2	0	+0.8	−0.5	–	+2.5
200	+0.1	0	+0.6	–	–	+2.5

surface water temperatures along the west coast of Vancouver Island generally increase during the period from May to July or August (Fig. 13; Pickard and McLeod, 1953) it is surprising to note that in Muchalat and Tahsis the May (1959) temperatures were higher than the July (1933) ones. Meteorological records (Anon., 1933, 1955–1960) indicate that in the first part of 1959 the mean air temperature on the west coast of Vancouver Island was about 0.3 C° above the long-term average whereas in 1933 it was about 1.1 C° below the average. During the first part of 1960 the mean air temperature was close to the long-term average. Although these air temperature differences agree in direction with the water temperature changes they appear to be insufficient in magnitude as the average increase in surface water temperature from May to June is about 2 C° and from June to July about 1.5 C° (Fig. 13).

In 1959 and 1960 the salinity values at all depths in this group of inlets (except at 200 m in Tlupana) were less than in 1933. In the surface layer this was possibly because the river runoff might be expected to be larger in May and

June than in late July (see Fig. 4). At greater depths the salinity differences may be indicative of the temporal variations that occur in these inlets. In dissolved oxygen the (1959 minus 1933) and the (1960 minus 1933) differences are generally much the same as the (1960 minus 1959) values. In Fig. 6 and 7 it will be seen that in the inner basins of all three inlets the dissolved oxygen values are low, suggesting limited circulation, but the fact that all the water properties do show some changes suggests that some influx of outside water takes place frequently, i.e. at intervals of the order of a year, although large-scale flushing may be less frequent.

The distributions of properties along the lengths of the inlets were of the same character in 1933 as in 1959 and 1960.

6.33 NEROUTSOS INLET

Waldichuk (1958) gave some information on the oceanographic characteristics of Neroutsos proper during August 1957 and compared his data with the findings of Hutchinson and Lucas (1927) in August 1927. He remarked that the distributions of salinity and temperature in the deep water were not especially different in 1957 from 1927, but that in the upper 10 m salinities were less by 1‰ in 1957 compared to 1927. He compared the oxygen values by a series of profiles which indicate that the main differences consisted of substantially lower values from the surface to 5 m depth near the inlet head in 1957 than in 1927, with higher values in 1957 at 10 m and minor differences below this.

The approximate differences between the 1959 and 1957 data and between the 1959 and the 1927 data are summarized in Table VII. These are averages of values at five stations which among themselves show significant differences. They suggest that in 1959, as compared to 1927, there were rather higher salinities, lower temperatures and lower dissolved oxygen values in the upper 20 m, with higher values for oxygen below this. In 1959 both the salinities and the temperatures were lower than in 1927. The lower temperatures in 1959 may be attributed to the observations being made in June before the seasonal temperature maximum which may be expected to be in August (see Fig. 13 for average surface temperature values at Kains Island at the mouth of Neroutsos).

The Hutchinson and Lucas values for oxygen content in the deep water were for bottom samples only. As it is not uncommon in the inlets to find low oxygen values close to the bottom, even when the main body of the water is well aerated, it is possible that their low values which give rise to the large differences of 2.5 ml/l at 100 and 200 m may not be representative of the main body of the deep water.

It was stated earlier (Section 4) that Waldichuk had suggested that low oxygen values in the outer basins of Neroutsos might be a consequence of the inflow of upwelled, low-oxygen Pacific Ocean water. This suggestion will now be examined.

Lane (1962) has shown that to the southeast along the Vancouver Island coast (off Amphitrite Point) subsurface, dense water upwells and moves on to the shelf in summer. This is probably the source of the deep water in the southern

inlets and a similar process may occur off Neroutsos. To examine the possibility, the deep water properties at the outer stations of Neroutsos (Sta. 9 and 8) were noted and then the previous occurrences of water of similar properties over the continental shelf outside Neroutsos were sought in the Data Records of the Pacific Oceanographic Group (Anon., 1957a–59). Particular attention was paid to water with a dissolved oxygen content similar to that of the deep water at the outer stations in Neroutsos, i.e. about 3.4 ml/l. (For convenience this will be referred to as '3.4 ml/l water'.) The deep water characteristics in Neroutsos (outer sill depth 78 m) are shown in Table VIII together with the depth and other characteristics of water with an oxygen content close to 3.4 ml/l outside Neroutsos.

TABLE VIII. Water properties in the outer basins of Neroutsos Inlet in 1959 and over the continental shelf outside in 1957, 1958 and 1959.

Cruise	Station	Date	Sample depth	Temperature	Salinity	σ_t	Dissolved oxygen content
			m	°C	‰		*ml/l*
	University of British Columbia:						
59/6	NER 8	May 1959	196	7.24	33.37	26.13	3.44
	125 m inner sill depth between NER 8 and NER 9.						
59/6	NER 9	May 1959	125	7.07	33.53	26.28	3.34
	78 m outer sill depth.						
	Pacific Oceanographic Group cruises with stations over the continental shelf off the west coast of Vancouver Island:						
C-57-1	Sta. 55	May 1957	74	7.10	33.10	26.10	4.12
			99	7.00	33.82	26.51	2.63
C-57-2	Sta. 58	July 1957	74	7.39	33.50	26.21	3.90
			98	7.30	33.77	26.43	2.94
C-57-3	Sta. 55	Oct. 1957	98	7.53	33.22	25.97	4.51
			123	7.67	33.65	26.28	3.28
C-57-4	Sta. 55	Nov. 1957	87	7.95	33.19	25.88	4.01
			130	7.40	33.69	26.36	3.20
NorPac	Sta. 16	Mar. 1958	125	7.25	33.37	26.13	4.51
			150	7.22	33.69	26.37	3.40
NorPac	Sta. 14	July 1958	48	7.39	33.40	26.12	3.53
			73	6.87	33.76	26.48	2.97
CS-58-1	Sta. 93	Dec. 1958	124	7.69	33.43	26.11	3.49
			149	7.50	33.58	26.25	3.24
NorPac	Sta. 12	Jan. 1959	114	8.28	33.54	26.11	3.40
			137	8.08	33.61	26.19	3.22
			182	8.05	33.70	26.27	2.78
CS-59-1	Sta. 37	Apr. 1959	173	7.28	33.46	26.19	3.99
			197	7.22	33.59	26.30	4.13
			247	6.36	33.88	26.64	3.66
			296	5.78	33.92	26.75	2.86
CS-59-2	Sta. 41	June 1959	150	6.56	33.72	26.49	3.76
			175	6.44	33.85	26.61	3.24

The station used from each Pacific Oceanographic Group cruise was that closest to Neroutsos at which '3.4 ml/l water' occurred. The stations were west of Quatsino Sound or off Cape Cook (Fig. 1).

It is seen from the data in this Table that the depth of occurrence of the '3.4 ml/l water' varied considerably from cruise to cruise. There was some indication of the low-oxygen content water upwelling to shallower depths in the summer but no clear seasonal cycle is obvious off Neroutsos. In the Table it will be seen that in 1959, prior to the University of British Columbia cruise, the '3.4 ml/l water' was recorded in April between 247 and 296 m depth and in January at 114 m depth. However, in neither case were both the temperature and salinity the same as in the deep water in Neroutsos. In 1958, '3.4 ml/l water' with temperature and salinity values similar to those at Sta. 9 could have been present in July between 48 and 73 m. In March 1958 the temperature of the outside '3.4 ml/l water' was similar to that at Sta. 8 but the salinity was greater. In May 1957 '3.4 ml/l water' similar to that at Sta. 9 could have been present between 74 and 99 m.

It is possible that the deep water in Neroutsos in 1959 might have had a higher oxygen content than 3.4 ml/l when it entered, the value decreasing during its residence in the inlet to the 3.4 ml/l value observed in 1959. For instance, in March 1958 the water at 125 m outside Neroutsos had the same temperature as that at Sta. 8 in 1959 but had the higher oxygen content of 4.51 ml/l.

Summarizing, on the basis of the evidence presented above it appears unlikely that the deep water in the outer basins of Neroutsos in May 1959 could have entered over the 78 m outer sill in 1959 but could have entered in 1958 or 1957.

7. SUMMARY

Tully (1937) in his study of the Nootka Sound inlets drew attention to the seaward movement of the low-salinity surface layer in those inlets and later (1937), from his study of Alberni, he developed the idea of the estuarine circulation consisting of the surface outflow with compensating subsurface inflow of saline water to maintain continuity of volume. Subsequent observations by Waldichuk (1958) indicated that Neroutsos also possessed such a circulation. The University of British Columbia study of 1959 to 1961 described in the present paper recorded observations in the five Vancouver Island inlets previously examined and extended them to nine other inlets, so that with Northcote's observations in Nitinat all the inlets of 10 miles length or more in the west coast of Vancouver Island have now been examined.

The observations indicate that an estuarine circulation probably exists in all of these inlets. That the thickness of the low-salinity surface layer was generally less and the salinity greater in the Vancouver Island inlets than in the mainland ones (Pickard, 1961) is attributed to the small river runoff in Vancouver Island. Low values for dissolved oxygen were more common in the Vancouver Island inlets than in the mainland ones; this is taken to indicate a less rapid estuarine circulation in the former because of the smaller river runoff.

An unusual temperature distribution was observed in Tofino where the temperature increased by nearly 6 C° from 30 to 85 m depth in contrast to the general trend in the inlets for it to decrease from the surface to the deeper water.

An examination of the relations between the deep water characteristics, the sill depths of the inlets and the ocean water characteristics suggests that the deep water in the inlets is probably replaced, at least in part, in the latter part of each year when the ocean water reaches its maximum density above the sill depths.

Very few oceanographic observations in the winter are available for the Vancouver Island inlets, so that the annual cycle of water property changes and the possible effect of the winter runoff maximum (in contrast to the summer maximum in the mainland inlets) still remains to be described.

8. ACKNOWLEDGMENTS

The author wishes to acknowledge assistance from many sources.

The work was a part of a programme of oceanographic research supported by the National Research Council of Canada under Block Term Grant BT-100.

The observations were made chiefly from C.N.A.V. *Whitethroat* made available by the Royal Canadian Navy through the Pacific Naval Laboratory, Esquimalt, B.C., with additional work in Tofino from the Department of Fisheries vessels *Laurier* and *Atolla*. The material assistance rendered by the officers and crews of each of these vessels is acknowledged.

The Canadian Hydrographic Service, Victoria, B.C. of the Department of Mines and Technical Surveys, through Mr R. B. Young, Regional Hydrographer, made available for reference their detailed field sheets from surveys of inlets in Vancouver Island.

The greater part of the field work was carried out under the author's direction by student assistants associated with the Institute of Oceanography, while most of the figures were drawn by Mr T. H. Killam.

The author expresses his sincere thanks to these organizations and individuals, and particularly to Dr M. Waldichuk of the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C. for making available unpublished data for some of the Vancouver Island inlets and for reading the manuscript and offering helpful suggestions, to Dr J. P. Tully for his critical review of the manuscript, and to Dr T. G. Northcote, Institute of Fisheries, University of British Columbia for making available his data on Nitinat Lake.

9. REFERENCES

ANON. 1933. Monthly record of meteorological observations in Canada and Newfoundland. Canada Department of Marine, Meteorological Service, Toronto.

MS, 1953. Observations of sea water temperature and salinity on the Pacific coast of Canada, Vol. 12, 1952. Fisheries Research Board of Canada, Nanaimo, B.C. 64 pp.

1955–60. Monthly record, meteorological observations in Canada. Canada Department of Transport, Meteorological Branch, Toronto.

MS, 1957. Physical and chemical data record, Alberni Inlet and Harbour, 1939 and 1941. Fisheries Research Board of Canada, Nanaimo, B.C. 89 pp., 7 fig.

1957–59. Data Records. *Fish. Res. Bd. Canada, MS Rept. (Oceanogr. and Limnol.)*, Nos. 16, 17, 29, 36, 43, 47, 52.

MS, 1959. British Columbia Inlet Cruise, 1959. Data Report No. 15, Institute of Oceanography, University of British Columbia, Vancouver, B.C. 29 pp. 2 fig.

1960a. Surface water supply of Canada, Pacific drainage, British Columbia and Yukon Territory. Climatic years 1956–57 and 1957–58. Canada Department of Northern Affairs and National Resources, Water Resources Paper No. 124, 642 pp. Ottawa. [Also earlier papers referred to therein.]

MS, 1960b. British Columbia Inlet Cruise, 1960. Data Report No. 17, Institute of Oceanography, University of British Columbia, Vancouver, B.C. 37 pp., 4 fig.

MS, 1961. British Columbia Inlet Cruises, 1961. Data Report No. 19, Institute of Oceanography, University of British Columbia, Vancouver, B.C. 62 pp., 3 fig.

1962a. Information Bulletin No. 13, February, 1962. Nautical charts etc. covering the southern British Columbia coast including Vancouver Island. Canadian Hydrographic Service, Department of Mines and Technical Surveys, Ottawa.

1962b. Pacific coast tide and current tables. Canadian Hydrographic Service, Department of Mines and Technical Surveys, Ottawa. 250 pp.

DEFANT, A. 1961. Physical oceanography. Pergamon Press, Oxford. 1327 pp.

HERLINVEAUX, R. H. 1962. Oceanography of Saanich Inlet in Vancouver Island, British Columbia. *J. Fish. Res. Bd. Canada*, **19**(1): 1–37.

HOLLISTER, H. J. 1960. Observations of seawater temperature and salinity on the Pacific Coast of Canada, Vol. 19, 1959. *Fish. Res. Bd. Canada, MS Rept. (Oceanogr. and Limnol.)*, No. 67, 97 pp., 31 fig.

HUTCHINSON, A. H., AND C. C. LUCAS. MS, 1927. Report on the waters of Quatsino Sound, Alice Arm. The effect of the pulp mill at Port Alice, 1927. *Fish. Res. Bd. Canada, MS Rept. Biol. Sta.*, No. 324, 11 pp., 3 tables.

LAFOND, E. C., AND R. S. DIETZ. 1948. New snapper-type sea floor sediment sampler. *J. Sedimentary Petrology*, **18**: 34–37.

LANE, R. K. 1962. A review of the temperature and salinity structures in the approaches to Vancouver Island, British Columbia. *J. Fish. Res. Bd. Canada*, **19**(1): 45–91.

PICKARD, G. L. 1961. Oceanographic features of inlets in the British Columbia mainland coast. *J. Fish. Res. Bd. Canada*, **18**(6): 907–999.

PICKARD, G. L., AND D. C. MCLEOD. 1953. Seasonal variation of temperature and salinity of surface waters of the British Columbia coast. *J. Fish. Res. Bd. Canada*, **10**(3): 125–145.

PRITCHARD, D. W. 1952. Estuarine hydrography. Advances in Geophysics. Volume I, pp. 243–280. Academic Press Inc., New York. 362 pp.

TULLY, J. P. 1937. Oceanography of Nootka Sound. *J. Biol. Bd. Canada*, **3**(1): 43–69.

1949. Oceanography and prediction of pulp mill pollution in Alberni Inlet. *Bull. Fish. Res. Bd. Canada*, No. 83, 169 pp.

WALDICHUK, M. 1956. Basic productivity of Trevor Channel and Alberni Inlet from chemical measurements. *J. Fish. Res. Bd. Canada*, **13**(1): 7–20.

1958. Some oceanographic characteristics of a polluted inlet in British Columbia. *J. Mar. Res.*, **17**: 536–551.

MS, 1962. Unpublished oceanographic data for Alberni Inlet for 1954, 1957, 1959 and 1961. Fisheries Research Board of Canada, Nanaimo, B.C.

Glycolysis in Lingcod Muscle During Frozen Storage[1]

By N. Tomlinson, R. E. E. Jonas and S. E. Geiger

Fisheries Research Board of Canada
Technological Research Laboratory, Vancouver 8, B.C.

ABSTRACT

The lactic acid content and several acid-soluble phosphorus-containing fractions of lingcod muscle have been measured after periods of storage of up to 6 months at storage temperatures between 0 and −30°C. The fish were killed in an unexercised condition and frozen either in liquid nitrogen or at the temperature of storage. Glycolysis, as indicated by lactic acid accumulation, clearly proceeded at temperatures down to and including −20°C, and some evidence was obtained to indicate that it may proceed at a very low rate indeed (of the order of 0.5 μmole lactic acid formed/g of muscle/month, or less) at a temperature of −30°C. Acid-labile and acid-soluble phosphorus decreased during storage at temperatures down to and including −20°C in muscle frozen by either procedure, but only in the more slowly frozen muscle at −30°C. Acid-stable and acid-soluble phosphorus decreased at temperatures down to −20°C, but not at −30°C.

INTRODUCTION

Of the various factors that influence the course of changes in the quality of fish muscle during frozen storage, the condition of the fish at the time of freezing appears to be among the most important (Love, 1962a, b; Love and Haraldsson, 1958; Nishimoto and Tanaka, 1960; Piskarev *et al.*, 1958; for earlier references see review by Dyer and Dingle, 1961). One aspect of condition which has been given attention by several investigators is that associated with *rigor mortis*, for the stage of *rigor mortis* in which a fish is frozen may affect the denaturation of protein and the development of toughness in the muscle during storage (e.g. Reay, 1960; Love, 1962b), and can influence the occurrence of "thaw rigor" with its accompanying undesirable drip (Amano *et al.*, 1955). The consideration of such facts has lead naturally to the investigation of certain biochemical processes associated with *rigor mortis* (e.g. glycolysis and the decomposition of adenine nucleotides and phosphocreatine) as they occur in frozen fish muscle, and particularly the influence of storage temperature on the course of these processes.

Amano *et al.* (1955) found that "thaw rigor" occurred in fish killed in an unexhausted condition and frozen quickly, but not in exhausted fish similarly frozen. In the unexhausted fish, quite high concentrations of ATP (measured as AL-P)[2] and glycogen were present in the muscle when thawing began and these were rapidly destroyed with the production of IMP and lactic acid during thawing and development of "thaw rigor". Amano *et al.* indicated that it would not be

[1]Received for publication February 27, 1963.

[2]Abbreviations used: ATP, ADP and AMP for adenosine triphosphate, adenosine diphosphate, and adenosine monophosphate, respectively; IMP for inosine monophosphate; AL-P for acid-labile and acid-soluble phosphorus. AL-P and other abbreviations used to indicate certain phosphorus fractions of the muscle are described in detail under "Methods and Materials".

J. Fish. Res. Bd. Canada, **20**(5), 1963.
Printed in Canada.

necessary to avoid prerigor freezing of fish, as "thaw rigor" did not occur after the fish had been stored about 2 weeks at −15°C. Although the reason for this was apparently not investigated, it seems likely from the findings of Tanaka and Tanaka (1955) with whale meat that it resulted from the destruction of ATP in the muscle during storage at −15°C.

Heen (1953) found that AL-P was lost more quickly from fish muscle during freezing in air at −17°C than it was in muscle stored at 0°C. Saito and Hadaka (1956) also observed rapid loss of AL-P from fish muscle during freezing in air at −20°C, and in addition found that there was a very rapid loss of AL-P from muscle at the time of thawing. Similarly, Saito and Arai (1957a, b) observed that ATP and ADP were rapidly degraded with the formation of IMP in carp muscle during slow freezing at −8°C, the process in fact proceeding more quickly under these conditions than it did in muscle stored at 0 or 16°C. During subsequent storage of the slowly frozen muscle for a period of 100 days at −8°C, the small residues of ATP and ADP still present in the muscle after freezing gradually decreased, and IMP was degraded with the formation of inosine and hypoxanthine. Partmann (1961a, b) demonstrated that in the white body muscle of carp and rainbow trout frozen quickly in liquid air, AL-P was destroyed more quickly during subsequent storage of the frozen muscle at temperatures between −2 and −4°C than it was at temperatures of −8°C or lower, and also more quickly than in muscle stored at 0 or 10°C that had not been subject to freezing. At −8°C, AL-P was reduced to about 10% of its initial concentration in the muscle in 10–20 days, while at −24°C there was little if any detectable change in its concentration in 180–220 days. Bito and Amano (1962) studied the influence of temperatures near −2°C on the course of breakdown of ALP in fish muscle and also the accelerating effect of freezing. In all the work described above in this paragraph, the fish used were apparently in a relatively rested state when killed. On the other hand, Jones and Murray (1961) have examined in detail the changes that occurred in the nucleotides of the muscle of trawl-caught cod frozen in liquid nitrogen and stored at several temperatures down to −30°C. Little ATP or ADP was present in the muscle of these fish at the time of freezing, and a small resynthesis of ATP followed by a partial destruction was detected at each temperature (−14, −20 and −30°C). Inosine increased at −14 and −20°C, but there was little change at −30°C. Hypoxanthine was formed only at the higher temperature. Sawant and Magar (1961) have reported the degradation of ribonucleotides beyond the stage of dephosphorylation in the muscle of surmai and mackerel frozen *post rigor* and stored at −15°C.

The fact that glycolysis can proceed slowly in fish muscle at a temperature as low as −10°C was demonstrated by Sharp (1934). In addition, Sharp (1935) found that in frozen fish muscle the maximum rate of glycolysis occurred between −3.2° and −3.7°C, and also that the freezing of muscle at temperatures below −2°C brought about some change that resulted in a very rapid formation of lactic acid when the muscle was thawed. Certain observations by Partmann (1961b) of *post mortem* changes in the pH of fish muscle appear to be in agreement with Sharp's findings regarding the rate of glycolysis at temperatures above −10°C.

At −24°C Partmann found there was no change in the pH of carp muscle during a storage period of 120 days. In cod and haddock stored at temperatures of −10 and −18°C, van den Berg (1961) found a decrease in muscle pH occurred during the first 1–2 months of storage, after which it increased to about the initial value. As these last fish were obtained from the market before freezing, it is improbable that the decrease in pH should be attributed to glycolysis.

Little information is available regarding breakdown of phosphocreatine during frozen storage of fish muscle, but Heen (1953) found it to be rapidly destroyed during slow freezing in air at −17°C, and Saito and Arai (1957c) have made a similar observation.

In the present work, changes in the various fractions of the acid-soluble phosphorus compounds and in the lactic acid content of the muscle of lingcod during frozen storage at temperatures between 0 and −30°C have been investigated. The fish were killed in an unexercised condition and frozen either very quickly in liquid nitrogen or more slowly at the temperature of storage.

MATERIALS AND METHODS

Lingcod (*Ophiodon elongatus*) weighing about 1.5 kg each were captured alive by dragging off the mouth of the Fraser River near Steveston, B.C. They were held alive at the Vancouver Public Aquarium in circulated sea water at 10°C until required. Some of these fish ate while in captivity, others would not. This is indicated in the Tables. Fish were killed by a heavy blow on the head, filleted and skinned. The lateral dorsal muscle was then cut crosswise into pieces about ½ inch thick. When muscle was to be frozen in liquid nitrogen prior to storage, the fish were killed and the pieces of muscle were frozen at the Public Aquarium, the whole process from catching the fish to the completion of freezing taking about 5 minutes. The frozen muscle was transported to the laboratory in an insulated box containing dry ice and was then placed in storage at the desired temperature. The muscle would thus be placed in storage about 1½ hours after the fish was killed. When muscle was to be frozen at the temperature of storage, fish were transported to the laboratory in well-aerated sea water chilled to 3–4°C. Under these conditions the fish struggled little except during catching and placing in the transport tank, a procedure requiring 30 seconds or less. Pieces of muscle to serve as controls from these latter fish were frozen immediately in liquid nitrogen, while the remaining pieces were allowed to freeze on metal shelves against the refrigerant coils in the storage cabinets. In this way all pieces reached storage temperatures within 24 hours, so that measurements made from the end of the first day of storage onward reveal any changes occurring in the muscle at these temperatures. Analyses of controls were carried out on the day of killing, the control pieces being packed in dry ice after freezing until they could be extracted. All pieces were stored in closed polyethylene bags after being frozen. Samples analyzed (5 g each) were not allowed to thaw prior to extraction. Methods of analysis have been described previously (Tomlinson *et al.*, 1961). For convenience, the description of the various phosphorous fractions measured, and the abbreviations used to designate them in the Tables and text, are repeated here.

I-P. Inorganic Phosphorus Fraction

ML-P. Molybdate-labile Phosphorus Fraction

This fraction is probably derived chiefly from phosphocreatine, but the phosphorus of certain other compounds (e.g. ribose-1-phosphate and acetyl phosphate) would also appear here in addition to a small percentage of the phosphorus of several other compounds (e.g. ATP).

AL-P. Readily Acid-hydrolyzable Phosphorus Fraction

In muscle in which the phosphorus of this fraction is present at a relatively high concentration (e.g. in muscle from freshly killed, unexercised fish) the phosphorus is derived principally from ATP, with relatively small contributions from other compounds (e.g. ADP, hexose diphosphate, glucose-1-phosphate). As the phosphorus in this fraction decreases *post mortem* the proportion contributed by ATP also becomes reduced.

AS-P. Acid-stable Phosphorus Fraction

This includes the phosphorus of AMP, IMP, the acid stable P of ATP and ADP, of various phosphorylated sugars and possibly other compounds.

RESULTS AND DISCUSSIONS

The results of two representative experiments in which muscle was frozen at the temperature of storage are presented in Table I, while in Table II the results of a representative experiment with muscle frozen in liquid nitrogen before storage are recorded. The fish used in the early part of this work, in which the muscle was frozen at the temperature of storage, ate while in captivity; but in the later work, in which muscle was frozen in liquid nitrogen, the fish used refused to eat. This difference probably contributed to the rather large differences observed between individual fish in some of the components measured, particularly in the quantity of AL-P found in the muscle when the fish were killed, and the maximum quantity of lactic acid that accumulated during storage. The muscles of feeding fish were higher in each of these components than were those of the non-feeding ones. However, fairly large differences were also observed between individual fish within the 2 groups — the magnitude of the differences being of the order indicated by the data for the 2 fish in Table I. In individual fish in the feeding group, agreement between duplicate samples was quite good (rarely deviating by more than $\pm 5\%$), except for ML-P which, in both groups of fish, contained little phosphorus and was very variable. In the non-feeding fish, variations between individual samples from one fish, with the exception of ML-P, tended to be somewhat more variable than for the feeding fish. The magnitude of the variations is indicated in Table II. Although variations as great as those indicated for AS-P and lactic acid were not found in all the fish, variations somewhat greater than those indicated for AL-P were found in some. The findings may be summed up thus:

(1) Glycolysis, as indicated by lactic acid accumulation, after the first day of storage in fish frozen at the temperature of storage and from the time of storage in fish frozen in liquid nitrogen, clearly proceeded at temperatures down to and

TABLE I. Influence of various storage temperatures on changes in the lactic acid content and in the acid-soluble, phosphorus-containing fractions of slowly frozen lingcod muscle.[1]

Temperature and time of storage		mg P per gram of muscle				Lactic acid
		I-P	ML-P	AL-P	AS-P	mg/g muscle
°C	*Days*					
Fish 1						
–	0	.91	.15	.64	.43	1.16
20	1	1.96	.11	.11	.05	5.01
0	1	1.66	.10	.11	.28	5.44
	7	2.08	.01	.14	.14	6.91
–3	1	1.61	.18	.08	.41	6.21
	7	1.80	.12	.09	.23	6.48
	15	1.96	.14	.11	.17	6.98
	28	2.04	.09	.13	.13	6.54
–6	1	1.49	.07	.28	.37	5.19
	7	1.86	.07	.09	.38	7.45
	15	1.81	.04	.09	.31	6.75
	28	1.74	.06	.07	.32	7.16
	62	1.82	.04	.09	.29	6.57
–10	1	1.18	.04	.63	.42	3.38
	7	1.32	.10	.48	.34	4.96
	15	1.41	.09	.42	.33	5.42
	28	1.77	.06	.25	.29	5.49
	62	1.88	.04	.12	.38	5.31
–30	1	1.14	.04	.58	.39	2.32
	7	1.21	.03	.58	.45	2.36
	15	1.18	.05	.50	.45	2.16
	28	1.28	.04	.53	.47	2.68
	62	1.26	.02	.49	.45	2.24
Fish 2						
–	0	1.22	.10	.46	.48	1.36
–10	1	1.35	.09	.46	.43	3.80
	7	1.75	.04	.23	.34	5.60
	33	1.87	.09	.11	.26	5.10
	92	2.02	.10	.09	.08	4.17
–20	1	1.29	.06	.43	.46	2.58
	7	1.38	.03	.43	.51	3.42
	33	1.63	.07	.33	.44	3.53
	92	1.67	.07	.28	.27	5.04
–30	1	1.46	.00	.38	.48	2.66
	7	1.50	.02	.30	.53	2.64
	33	1.40	.00	.28	.43	2.52
	92	1.52	.09	.19	.45	2.58

[1]The fish used in this work ate well in captivity and were killed in an unexercised condition. Control samples frozen in liquid nitrogen, all others at temperature of storage (see Methods and Materials). Values recorded are averages for duplicate samples for zero time controls and for single samples at other times.

TABLE II. Influence of various storage temperatures on changes in the lactic acid content and in the acid-soluble, phosphorus-containing fractions of lingcod liquid-nitrogen-frozen muscle.[1]

Temperature and time of storage		mg P per gram of muscle				Lactic acid
		I-P	ML-P	AL-P	AS-P	mg/g muscle
°C	*Days*					
	0					
–	(average)	1.346	.016	.318	.549	1.44
	(range)	1.272–1.405	.006–.04	.296–.358	.473–.615	1.17–1.86
–10	2	1.523	.022	.282	.635	2.41
	14	1.752	.007	.090	.640	3.23
	30	1.799	.026	.015	.506	3.25
–20	2	1.323	.100	.331	.560	1.32
	30	1.399	.033	.321	.686	1.95
	97	1.388	.156	.235	.580	2.91
	184	1.607	.047	.181	.409	2.52
–30	2	1.390	.072	.310	.477	1.39
	30	1.343	.033	.309	.561	1.43
	97	1.151	.120	.303	.514	1.52
	184	1.283	.036	.390	.508	1.65

[1]The fish used in this experiment had been held in captivity without eating about 1 month before being killed. All samples were frozen in liquid nitrogen prior to storage. The values recorded for the zero time controls are for 4 samples, all others are averages for duplicate samples.

including –20°C in muscle frozen by either procedure. However, in muscle frozen and stored at –30°C no formation of lactic acid was detected (during 90 days storage) while in muscle frozen in liquid nitrogen and then stored at –30°C a very small formation of lactic acid was detected in the muscle from 3 of 6 fish examined. The rate of formation in these 3 fish was of the order of 0.04 mg of lactic acid formed/g of muscle/month, or less. In the other 3 fish frozen in liquid nitrogen the average values for lactic acid were 1.27 mg/g muscle when frozen and 1.11 mg/g after 180 days of storage. In each of these last 3 fish, 2.5 to 3.2 mg lactic acid/g muscle accumulated during storage at the higher temperatures, demonstrating that apparent absence of lactate formation at –30°C was not the result of lack of precursor.

(2) Results with ML-P were disappointing. Only small amounts of phosphorus were found in this fraction at the time of killing and no clear trend in changes in the fraction during storage was observed. That such low quantities of ML-P are not necessarily characteristic of lingcod muscle has been indicated by observations made in separate work. When a lingcod was held at 0°C in well-aerated water for about 1 hour prior to killing, the muscle — frozen in liquid nitrogen — was found to contain ML-P in a concentration (0.39 mg P/g muscle) only a little less than that of AL-P. As has been observed by others (*vide ut supra*) a rapid loss of ML-P occurred during freezing of muscle from this fish at –30°C.

(3) AL-P was degraded at temperatures down to −20°C in muscle frozen by either procedure, but while the phosphorus found in this fraction decreased slowly in muscle frozen and stored at −30°C, no decrease was detected in muscle frozen in liquid nitrogen and then stored at this temperature. In fact an apparent increase was found to occur in the latter part of the storage period in all muscle samples (from 6 fish) stored in this manner. The source of this apparent increase is not known.

(4) AS-P was degraded at −10°C and at −20°C in muscle frozen by either procedure. Although not shown in the example given in Table II (in which storage at −10°C was discontinued after 30 days), AS-P has been found to be reduced by about 30% in 180 days in muscle stored at this temperature after being frozen in liquid nitrogen. There is no clear evidence for any decrease in this fraction in muscle stored at −30°C when frozen by either procedure.

The data for fish 1 in Table I are in general agreement with earlier reports (see Introduction) regarding degradation of ATP and formation of lactic acid at temperatures between 0 and −10°C, but no loss of AL-P during freezing at −10°C was observed in the present work. Two possible explanations for this difference can be suggested. The fish used in the present work may have been exercised less before killing, and the samples of muscle frozen were perhaps smaller than those used in previous work and therefore may have been frozen more quickly. Evidence that glycolysis can proceed in fish muscle at a temperature as low as −20°C, and possibly at a very low rate indeed at −30°C, does not, as far as we are aware, appear to have been recorded previously, and would lend support to the suggestion of Jones and Murray (1961) that the resynthesis of ATP they observed in frozen cod muscle derived from glycolysis. In the present work, however, no evidence for net synthesis of AL-P (with the exception of samples frozen in liquid nitrogen and stored at −30°C) has been observed, even under conditions where glycolysis was proceeding actively. In fact the evidence indicates a net loss under such conditions. A *post-mortem* loss of AL-P from fish muscle, with or without an initial period of maintenance, has previously been observed to occur while glycolysis was proceeding (e.g. Tomlinson *et al.*, 1961; Fraser *et al.*, 1961). It may be possible that under conditions of frozen storage in which the muscle initially contains relatively high concentrations of AL-P, as occurred in the present work, a resynthesis such as that observed by Jones and Murray (1961) might be obscured. The changes in AS-P recorded are in agreement with the findings of Saito and Arai (1957b) and of Jones and Murray (1961) regarding the appearance of inosine in frozen cod muscle.

REFERENCES

AMANO, K., M. BITO AND M. SUYAMA. 1955. *Proc. 9th International Congress of Refrigeration*, Paris, **2**: 4.066–4.073.

BERG, L. VAN DEN. 1961. *Food Technol.*, **15**: 434–437.

BITO, M., AND K. AMANO. 1962. *Bull. Tokai Reg. Res. Lab.*, **32**: 149–153.

DYER, W. J., AND J. R. DINGLE. 1961. *In* Fish as Food. Edited by G. Borgstrom. Academic Press, New York, pp. 275–327.

FRASER, D. I., S. PUNJAMAPIROM AND W. J. DYER. 1961. *J. Fish. Res. Bd. Canada*, **18**: 641–644.

HEEN, E. 1954. Proc. Symp. Cured and Frozen Fish Tech., Sect. XV, Göteborg, Sweden (1953).

JONES, N. R., AND J. MURRAY. 1961. *Biochem. J.*, **80**: 26P-27P.

LOVE, R. M. 1962. *J. Sci. Food Agr.*, **13**: 534–545.
1962. *J. Food Sci.*, **27**: 544–550.

LOVE, R. M., AND S. B. HARALDSSON. 1958. *Nature*, **181**, p. 1334.

NISHIMOTO, J., AND K. TANAKA. 1960. *Mem. Fac. Fish., Kagoshima Univer.*, **8**: 70–74.

PARTMANN, W. 1961. *Naturwiss.*, **48**: 76–77.
1961. *Zeit. für Ernahrungswissenschaft*, **2**: 70–90.

PISKAREV, A., G. KRYLOV AND L. LUKYANITSA. 1958. *Kholodil'naya Tekh.* (*Moscow*) **4**: 48–52.

REAY, G. A. 1960. *Torry Research Station Annual Report 1960*. H. M. Stationery Office, Edinburgh, p. 9.

SAITO, K., AND T. HIDAKA. 1956. *Bull. Japan. Soc. Sci. Fisheries*, **21**: 1082–1085.

SAITO, T., AND K. ARAI. 1957. *Ibid.*, **22**: 569–573.
1957. *Ibid.*, **23**: 265–268.
1957. *Bull. Fac. Fish., Hokkaido Univer.*, **8**: 51–53.

SAWANT, P. L., AND N. G. MAGAR. 1961. *Food Technol.*, **15**: 347–350.

SHARP, J. G. 1934. *Proc. Roy. Soc. London Ser. B.*, **114**: 506–512.
1935. *Biochem. J.*, **29**: 850–853.

TANAKA, T., AND K. TANAKA. 1955. *Proc. 9th International Congress of Refrigeration*, Paris, **2**: 4.078–4.083.

TOMLINSON, N., E. S. ARNOLD, EVE ROBERTS AND S. E. GEIGER. 1961. *J. Fish. Res. Bd. Canada*, **18**: 321–336.

Composition and Palatability of Porbeagle Flesh[1]

By W. J. Dyer and D. I. Fraser

Fisheries Research Board of Canada
Technological Research Laboratory, Halifax, N.S.

AND

S. N. Tibbo

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

Frozen porbeagle (*Lamna nasus*) steaks from samples obtained under conditions typical of good and of poor handling were examined and their chemical composition determined. Lipid content was low, about 1% in the light muscle and 2% in the red. Phospholipase activity was absent, but considerable hydrolysis of triglyceride occurred. There was no ammonia production from the high urea content, 1.4–1.6%. Taste testing of cooked steaks showed only fair acceptability, an objectionable sour-to-bitter flavour being noted. Although its flavour may be relished by some, it is concluded that frozen porbeagle would not be generally acceptable to North Americans as a top-quality fisheries product.

INTRODUCTION

In recent years there have been frequent press reports that markets exist for presently unused fish species. One such species is the porbeagle, or mackerel shark (*Lamna nasus*), which is reported to be abundant along the Atlantic coast and is being caught and marketed chiefly by Norwegians.

Bigelow and Schroeder (1948) state that the centres of abundance for the porbeagle in the western Atlantic are along the outer coast of Nova Scotia and in the western part of the Gulf of Maine. Fishermen report it as the commonest large shark in summer along the Atlantic coast of Nova Scotia including Cape Breton.

The biology and abundance of the porbeagle are being studied by the Fisheries Research Board of Canada's Biological Station at St. Andrews, N.B. Exploratory fishing cruises in 1961 and 1962 in the Georges and Browns Banks areas showed that porbeagles were abundant (up to 16 fish per 100 hooks set) in both of these areas. The best catches were made with longlines set at the surface in areas where the surface temperatures were between 13 and 16°C.

To obtain data on composition and possible consumer reaction to this species, two specimens caught by this Board's research vessel *A. T. Cameron* in 1962 were frozen and portions transported to the Halifax Laboratory for chemical analysis and taste panel testing of cooked samples.

[1]Received for publication March 27, 1963.

J. Fish. Res. Bd. Canada, **20**(5), 1963.
Printed in Canada.

EXPERIMENTAL

Sample A was caught on September 15, 1962, on a floating longline at the entrance to the Bay of Fundy, about 3 miles east of Grand Manan Banks. Frozen squid was used as bait; the time of the set was 2.5 hr. This female shark had a fork length of 170 cm, with round and dressed weights of 56 and 33 kg, respectively. This sample was purposely treated as badly as might be expected under the worst commercial conditions. It was left on deck for 8 hr, dressed, left in the sun for 8 hr, and then held in a cool room at −1.1°C for 2 days before being frozen and held at −18°C.

Sample B was caught as above on September 11, 1962, on the western edge of Georges Bank, 3 to 4 miles north of Cultivator Shoal. The fork length of this male shark was 118 cm, and the dressed weight was 14 kg. This specimen received the best treatment possible under commercial conditions, being dressed 2–3 hr after catching, and placed at once into the freezing room on the *A. T. Cameron* in air at −18°C. It was transferred on September 18 to the freezing room at the St. Andrews Station (−18°C), and portions reloaded to the freezer room on the *A. T. Cameron* on September 29 along with Sample A. The samples were transferred to the cold storage room at the Halifax Laboratory (−26°C) on October 1, 1962, and examined October 9–12.

Steaks cut from the portion between the tail and the tail-end of the belly cavity were examined. The deep-seated dark red meat was almost completely absent in these portions of both samples, as has been reported by Braekkan (1959), who gives a good description of the distribution of red muscle in this species.

For the analyses, meat only from the dorsal portion of the steak, carefully separated from skin and depot fat, was chopped with a knife while still hard-frozen and thoroughly mixed.

Sample C, fork length 99 cm, was caught November 4, 1961, gutted, and held 4 days in ice on a trawler, then frozen and stored at approximately −22°C (−8°F) for $3\frac{3}{4}$ months at a local fish plant. Cross-sections of the meat, 3 cm in thickness, were sawn out at the point of insertion of the dorsal fin (thick part of the fish). The two portions of red muscle present in this section were separated and constituted 8.4% of the total weight of the steak. The white muscle was sampled as above.

Determinations of moisture, ash, total nitrogen (TN) and non-protein nitrogen (NPN), total lipid, free fatty acid (FFA), trimethylamine (TMA), trimethylamine oxide (TMAO) and tyrosine value were carried out as described previously (Mannan *et al.*, 1961). Phospholipid phosphorus was determined by the procedure of Harris and Popat (1954). An additional frozen sample was homogenized with cold 3% perchloric acid, followed by filtration and washing of the residue. Aliquots of the combined filtrates were taken for estimation of lactic acid (Barker and Summerson, 1941), ammonia nitrogen (Conway, 1962), and urea nitrogen (Hawk *et al.*, 1954). The perchloric acid extract was also used for precipitation of glycogen according to Carroll *et al.* (1956), followed by color development with the phenol-sulphuric acid reagent of Montgomery (1957).

While this work was in progress, Olley *et al.* (1962) reported the absence of phospholipase in Elasmobranch muscle. Therefore, phospholipid phosphorus (total phosphorus in the lipid extract) and FFA were determined in Samples A and B after storage for 5 months at −26°C to indicate whether phospholipid or triglyceride was the precursor of the FFA in the samples.

For the organoleptic testing of cooked Samples A and B only, portions of muscle of uniform size were cut from steaks 2 cm thick, excluding skin and bone. The still-frozen samples were baked in an oven at 500°F (260°C) for 18 minutes, and served immediately, without condiments, to a panel of 6 to 8 tasters. Taste panel procedure and method of scoring have been outlined previously (Dyer and Dyer, 1949; Dyer and Morton, 1956).

In order to obtain opinions more nearly approaching those of the consumer, steaks from the two frozen samples were cooked by Mrs Hickman, Department of Fisheries of Canada home economist for the Maritimes Area. Three cooking methods likely to be used in the home were employed: samples were baked, broiled and fried with added butter, salt and pepper, and tasted by the panel members.

RESULTS AND DISCUSSION

The composition of the flesh is shown in Table I. The porbeagle is a lean species with a total lipid content ranging from 0.8 to 1.2% in the white meat sampled, and 2.2% in the red meat. Braekkan (1959) finds 0.7 and 1.2%, respectively. The FFA content is rather high in all samples. At storage temperatures of −18 to −26°C for 24 to 28 days, the rate of FFA development appears to be more rapid than that observed by Olley *et al.* (1962) in another Elasmobranch species, the skate (*Raja maculata*), (124 mg per 100 g after 16 weeks at −14°C). The higher content of FFA in porbeagle is perhaps attributable to the slow freezing of the present samples, wherein muscle temperature would be maintained for a considerable period in the region just below the freezing point, where rapid lipid hydrolysis has been found to occur (Lovern and Olley, 1962).

TABLE I. Composition of porbeagle flesh.

	Sample A	Sample B	Sample C	
			White meat	Red meat
Moisture (%)	76.2	78.7	75.8	77.0
Total Lipid (%)	0.82	0.92	1.2	2.2
FFA (mg/100 g*)	128	129	323	326
TMA (mg N/100 g)	0.5	0.5	1.0	4.8
TMAO (mg N/100 g)	226	214	160	147
Tyrosine value (mg/100 g)	20	20	–	–
Glycogen (mg/100 g)	0	0	5	–
Lactic acid (mg/100 g)	959	738	712	–
Ammonia (mg N/100 g)	13.4	9.6	–	–
Urea (mg N/100 g)	747	670	–	–
NPN (%)	–	–	1.33	1.32

*M.W. of free fatty acid taken as 300.

Sample C, stored for 4 months at about −22°C, contained higher amounts of FFA; the amount present was the same in both white and red meat (325 mg/100 g), although the lipid content was higher in the latter.

Olley *et al.* (1962) have found that triglycerides rather than phospholipids were the exclusive precursors of free fatty acids in the Elasmobranch species studied. Assuming that lipid in excess of 0.7% is triglyceride (Olley *et al.*, 1962), there is sufficient triglyceride in the present samples to account for the FFA formed. In these samples phospholipid was not removed prior to titration, thus the values will be higher by the acidity of the acid phospholipids, and therefore, there is probably just sufficient triglyceride in Sample A. It was therefore desirable to determine whether phospholipid had decreased in the porbeagle flesh.

In Samples A and B free fatty acid had not changed during frozen storage for 5 months at −26°C, values of 125 and 131 mg per 100 g, respectively, being obtained. The phospholipid phosphorus content of both samples was 24.3 mg per 100 g fish. This indicates that phospholipid has not been hydrolyzed since Olley *et al.* (1962) show that the initial phospholipid content of all species examined was 18 to 28 mg phosphorus per 100 g (two Elasmobranchs contained 18 and 23 mg per 100 g). These results provide further confirmation that phospholipase is absent in Elasmobranch species.

Both the very low trimethylamine content and tyrosine values in the range normal for fresh fish indicate that no bacterial spoilage of the interior flesh had occurred in the samples. Ammonia values are slightly higher in Sample A, which was left longer prior to freezing, but are still within the range normal for fresh fish (Mannan *et al.*, 1961). It appears that no ammonia production from urea has occurred, even though the rather poor handling conditions would have been expected to provide ideal conditions for bacterial enzymic hydrolysis of the urea. Similarly, no ammonia developed from urea in the flesh of the dogfish (*Squalus suckleyi*) (Moyer *et al.*, 1959; Southcott *et al.*, 1960).

That the fish died by exhaustion is indicated by complete breakdown of muscle glycogen and the occurrence of very high lactic acid levels (0.7–0.9%). Trimethylamine oxide and urea levels are both high (1.2 and 1.6%, respectively) in Sample A, and 1.2 and 1.4% in Sample B, though the oxide is somewhat lower in Sample C, and also,slightly less in the red than the white meat. These values, higher than those in the Teleost fishes which also have no urea, are typical of Elasmobranch species, which are slightly hypertonic to the seawater in which they live. The trimethylamine oxide values are of the same order as the value of 200 mg N per 100 g previously reported (Dyer, 1952). This species, therefore, has an unusually high content of organic metabolites; urea, trimethylamine oxide and lactate contribute 3.4 and 3.7% in Sample A and Sample B, respectively. This accounts for the rather low moisture content found in the flesh of this non-fatty species (see discussion by Mannan *et al.*, 1961).

In Table II the proximate composition of the white and red muscle is compared with the data of Braekkan (1959). The data agree well. Red muscle appears to have a higher content of lipid as found with other species (Fraser

TABLE II. Proximate composition of white and red porbeagle muscle. (Total S_1 is sum of moisture, lipid, ash and crude protein (total N × 6.25). Total S_2 is sum of moisture, lipid, ash and protein (protein N × 6.25). Total S_3 is S_2 + lactate + urea + TMAO + other nitrogenous extractives (see text)).

Constituent (% wet weight)	Sample C		Data from Braekkan (1959)	
	White	Red	White	Red
Moisture	75.8	77.0	76.4	75.6
Lipid	1.2	2.2	0.7	1.2
Ash	1.3	1.2	1.5	1.6
Crude Protein	23.7	22.9	23.9	23.7
Total S_1	102.0	103.3	102.5	102.1
Protein	15.4	14.6		
Total S_2	93.7	95.0		
Lactate + urea + TMAO	3.1			
N extractives	2.2			
Total S_3	99.0			

et al., 1961). The total (S_2) is rather low, adding to only 93.7% in the white muscle of Sample C. The principal extractives are lactate (0.71%), TMAO (0.86%) and urea. The latter averages 1.52% on Samples A and B. NPN on Sample C, white flesh, is 1.33%. If the nitrogen of the TMAO (0.16%) and that of urea (0.71%) are subtracted, this leaves a total of 0.46% nitrogen as remaining nitrogenous extractives. Taking an average N content of 21% (Mannan *et al.*, 1961), this makes 2.2%. Thus the total composition is 93.7 + 3.1 + 2.2 = 99.0%. Not accounted for are the remaining non-nitrogenous extractives.

The total nucleotide content of the muscle, as estimated spectrophotometrically in perchloric acid extracts according to Szentkiralyi (1957), was 10.2 and 8.9 μmole per g in Samples A and B, respectively. Inosine compounds were found to constitute 87% of the total nucleotide in both samples. This is perhaps a consequence of struggling on the line, whereby the adenine compounds originally present in the rested living muscle are dephosphorylated and deaminated to inosine nucleotides. Subsequent decomposition to inosine and to hypoxanthine occurs, the rate of development of hypoxanthine depending on post-mortem handling conditions (Jones and Murray, 1962) and perhaps freezing rate as well. Accumulation of hypoxanthine, which has a bitter flavour (Jones, 1961), may therefore be responsible for the bitter flavour observed in the cooked samples as reported below. It is possible that faster freezing may lessen this factor.

Results of tests on baked samples, representing the averages of three panels, indicated little difference between the two samples, respective values being 53 and 55 for texture, 39 and 41 for taste, and 44 and 49 in overall grade for Samples A and B. With the numerical scoring system employed, ranging from 100 (perfect) to 0 (badly spoiled), freshly frozen fish of good initial quality normally achieve ratings of about 80. At a rating of 40 the samples are unacceptable to the panel. The low texture scores given the porbeagle may have been caused by the relatively slow freezing of the thick carcasses in air at −18°C. The

presence of an objectionable flavour, described as sour-to-bitter and noted by all tasters, resulted in lowered taste scores. An objectionable odour was evident during the cooking.

In the steaks prepared for the consumer-type tests, the objectionable cooking odour was again evident, and the sour-to-bitter flavour was noted in the cooked steaks. Some tasters found all samples poor to unacceptable; other grades ranged from fair to good depending on individual preference and cooking method. The overall opinion of most tasters was one of borderline acceptability. This is in agreement with the results reported above using the analytical taste panel technique on unseasoned baked samples. Frozen steaks were also prepared at home by several staff members exclusive of the taste panelists. Some reported a liking for the peculiar flavour; others were definite in their dislike. In conclusion, these experiments indicate that frozen porbeagle would not be generally acceptable to the Canadian public as a top-quality fish product of aesthetically pleasing character.

ACKNOWLEDGMENTS

The authors wish to thank Mrs Hickman for preparing the baked, broiled and fried samples for the consumer-type tests.

We are also indebted to J. R. Dingle, H. C. Freeman, R. J. Hoyle, Wanda Neal, P. H. Odense, Mabel Shiers and Margaret Scott for their interest and co-operation as members of the taste panel.

REFERENCES

BARKER, S. B., AND W. H. SUMMERSON. 1941. *J. Biol. Chem.*, **138**: 535–554.

BIGELOW, H. B., AND W. C. SCHROEDER. 1948. Part I, *Mem. Sears Found. Mar. Res.*, No. 1, pp. 112–123.

BRAEKKAN, O. R. 1959. *Fiskeridirektoratets Skrifter, Serie Teknologiske Undersokelser* III (8): 1–42.

CARROLL, N. V., R. W. LONGLEY AND J. H. ROE. 1956. *J. Biol. Chem.*, **220**: 583–593.

CONWAY, E. J. 1962. Micro-diffusion analysis and volumetric error, 5th ed. Crosby, Lockwood and Son, Ltd., London.

DYER, W. J. 1952. *J. Fish. Res. Bd. Canada*, **8**: 314–324.

DYER, F. E., AND W. J. DYER. 1949. *Ibid.*, **7**: 449–460.

DYER, W. J., AND M. L. MORTON. 1956. *Ibid.*, **13**: 129–134.

FRASER, D. I., A. MANNAN AND W. J. DYER. 1961. *Ibid.*, **18**: 893–905.

HARRIS, W. D., AND P. POPAT. 1954. *J. Am. Oil Chem. Soc.*, **31**: 124–127.

HAWK, P. B., B. L. OSER AND W. H. SUMMERSON. 1954. Practical physiological chemistry. 13th ed. The Blackiston Co., Inc., New York. p. 886.

JONES, N. R. 1961. *In*: Proceedings of Flavour Symposium. (Campbell Soup Co., Camden, N.J.), pp. 61–81. (Torry Memoir No. 64)

JONES, N. R., AND J. MURRAY. 1962. *J. Sci. Food Agric.*, **13**: 475–480.

LOVERN, J. A., AND JUNE OLLEY. 1962. *J. Food Sci.*, **27**: 551–559.

MANNAN, A., D. I. FRASER AND W. J. DYER. 1961. *J. Fish. Res. Bd. Canada*, **18**: 483–493.

MONTGOMERY, R. 1957. *Arch. Biochem. Biophys.*, **67**: 378–386.

MOYER, R. H., B. A. SOUTHCOTT, E. G. BAKER AND H. L. A. TARR. 1959. *J. Fish. Res. Bd Canada*, **16**: 791–794.

OLLEY, JUNE, R. PIRIE, AND HELEN WATSON. 1962. *J. Sci. Food Agric.*, **13**: 501–516.

SOUTHCOTT, B. A., R. H. MOYER, E. G. BAKER AND H. L. A. TARR. 1960. *J. Fish. Res. Bd. Canada*, **17**: 811–814.

SZENTKIRALYI, E. M. 1957. *Arch. Biochem. Biophys.*, **67**: 298–301.

Vertebral Numbers of American Plaice, *Hippoglossoides platessoides* (Fabricius), in the Northwest Atlantic[1]

By T. K. Pitt

Fisheries Research Board of Canada
Biological Station, St. John's, Nfld.

ABSTRACT

Vertebral numbers of American plaice in the Northwest Atlantic are compared. Counts ranged from 42 to 48 vertebrae excluding the urostylar half-vertebra.

No significant difference was found between vertebral averages of males and females.

Averages for an area extending from the Northeast Newfoundland Shelf southward over the whole of the Grand Bank and inshore to include St. Mary's Bay are statistically similar. The average for this area is significantly higher than averages fo the Gulf of St. Lawrence, the Labrador Shelf, Flemish Cap and Fortune Bay. However, over the whole area differences are not very great, the range of averages being (for a sample of 30 or more) 45.273–45.806 vertebrae.

The possible effects of differences in the time of spawning, larval drift and the inclusion of a large number of year-classes in the various samples are discussed as possible explanations for the low degree of variability in the whole area.

The vertebral averages of the year-classes 1942–1953 from St. Mary's Bay are not statistically different.

INTRODUCTION

The American plaice, *Hippoglossoides platessoides* (Fabricius), commonly known also as the dab or flounder, is one of the principal groundfishes of the Newfoundland area. In the Canadian area of the Northwest Atlantic the commercial fishery for this species was insignificant until 1948, but since that time production has gradually increased with the total landings from the Grand Bank in 1960 reaching 60 million pounds. Of this total 50 million pounds were landed in Canadian ports, with 33 million pounds being landed in Newfoundland ports alone. In the Northwest Atlantic the commercial fishery is carried out on the Grand Bank, the southern part of the Gulf of St. Lawrence, Georges Bank, and to a small extent on the Nova Scotian and St. Pierre Banks and in the area off Labrador. In this paper, samples have been included from all areas where this species has been taken in research cruises by the vessels operated by the St. John's Biological Station of the Fisheries Research Board of Canada; also a few samples from commercial trawlers are included. Figure 1 is a map of the area showing the place names used in the text.

All the vertebral counts were made by 2 persons, with at least 10% being checked by either the author or a senior member of the scientific staff of the Station. All whole vertebrae between, but not including, the basioccipital and the hypural bones were counted. An average of about 2% of the columns from each sample had fused vertebrae and were discarded. Less than half of these

[1]Received for publication February 15, 1963.

J. Fish. Res. Bd. Canada, **20**(5), 1963.
Printed in Canada.

fusions occurred in the last 3 caudal vertebrae. The vertebral numbers of the individual fish ranged from 42 to 48, but only 1 column was found with 42 and 1 with 43 vertebrae, so that the range was generally 44–48.

RELATION OF VERTEBRAL NUMBER TO SEX

From unpublished data on age readings of American plaice otoliths by the author, it is known that male plaice grow a little slower and mature at a younger age and smaller size than females; and also, fewer males than females are found

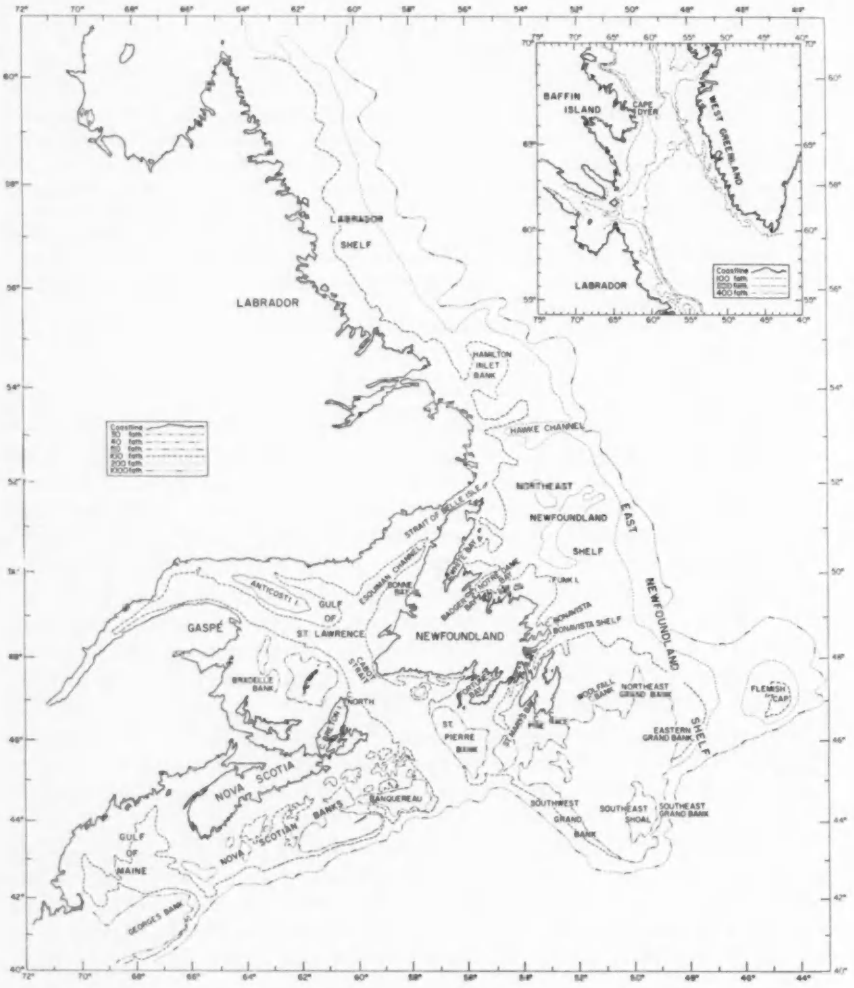


FIG. 1. Reference map showing most localities mentioned in the text.

TABLE I. Vertebral numbers of male and female American plaice from various areas of the Northwest Atlantic.

Area	Male											Female											Male–female
	42	43	44	45	46	47	48	No.	Av.	$S_{\bar{x}}$	S_x	42	43	44	45	46	47	48	No.	Av.	$S_{\bar{x}}$	S_x	
Labrador Shelf	...	...	4	19	17	...	...	40	45.325	0.656	0.104	...	...	9	94	110	10	...	223	45.543	0.649	0.065	−0.118
Hamilton Inlet Bank	...	...	16	131	177	22	1	347	45.599	0.691	0.037	...	...	13	148	182	23	...	366	45.587	0.664	0.037	0.012
NE Nfld. Shelf	...	...	9	91	124	15	...	239	45.607	0.664	0.042	...	...	12	136	187	25	...	360	45.525	0.664	0.035	0.072
White Bay	...	...	2	19	30	2	...	53	45.604	0.631	0.087	...	...	...	21	35	4	...	60	45.717	0.585	0.076	−0.113
Notre Dame Bay	...	...	2	58	73	7	...	140	45.607	0.608	0.051	...	...	3	55	58	7	...	126	45.548	0.640	0.057	0.059
Bonavista Shelf	...	...	2	28	46	6	...	82	45.683	0.646	0.071	...	...	9	114	163	22	1	309	45.650	0.670	0.038	0.033
NE Grand Bank	...	...	11	88	156	20	1	276	45.682	0.682	0.041	...	...	18	143	239	38	1	439	45.674	0.693	0.033	0.008
Flemish Cap	...	...	3	54	43	6	...	106	45.491	0.641	0.062	...	...	7	53	50	4	...	114	45.447	0.666	0.062	0.044
E Grand Bank	...	...	9	89	141	27	...	266	45.699	0.695	0.043	...	...	7	140	227	42	...	416	45.731	0.658	0.032	−0.032
SE Grand Bank	1	0	6	110	157	17	...	291	45.639	0.643	0.037	...	...	6	93	163	24	2	288	45.733	0.669	0.039	−0.094
SW Grand Bank	...	...	...	51	71	9	...	131	45.679	0.593	0.052	...	...	8	136	162	19	2	327	45.606	0.665	0.037	0.073
St. Mary's Bay	...	...	18	307	359	55	...	739	45.610	0.660	0.024	...	...	28	355	476	71	1	931	45.637	0.671	0.022	−0.027
Fortune Bay	...	...	1	17	24	...	...	42	45.548	0.550	0.085	...	1	5	33	32	4	...	75	45.427	0.757	0.087	0.121
St. Pierre Bank	...	...	2	34	47	3	...	86	45.593	0.602	0.065	...	...	3	48	68	4	...	123	45.593	0.598	0.053	...
Bonne Bay	...	...	1	23	20	4	...	48	45.563	0.681	0.098	...	...	2	24	33	3	...	62	45.597	0.639	0.081	−0.034
Port Saunders	...	...	7	106	108	10	...	231	45.524	0.631	0.042	...	...	8	107	115	9	...	239	45.523	0.627	0.041	0.001
Bradelle Bank	...	...	2	28	35	3	...	68	45.580	0.628	0.076	...	...	...	21	19	2	...	42	45.548	0.593	0.092	0.032
N of Anticosti	...	...	...	14	18	1	1	34	45.677	0.684	0.117	...	...	2	28	20	5	...	55	45.509	0.717	0.097	0.168
Gaspé	...	...	10	170	155	12	...	347	45.487	0.615	0.033	...	...	8	79	68	4	...	159	45.428	0.631	0.050	0.059
Off Cape North	...	...	2	22	13	3	...	40	45.425	0.712	0.113	...	...	2	12	13	2	...	29	45.517	0.738	0.137	−0.092
Banquereau	...	...	2	44	48	12	...	106	45.660	0.702	0.068	...	...	4	41	59	7	...	111	45.622	0.661	0.063	0.038
Total:	1	0	109	1,503	1,862	234	3	3,712	45.600	0.658	0.011	...	1	154	1,884	2,479	329	7	4,854	45.619	0.667	0.010	−0.019

after about age 15–16 years when the latter are a little over 45 cm in length. Thus, a sample of predominantly larger fish will have a large proportion of females and possibly bias the average if it should happen that the vertebral averages of the sexes are different.

Table I gives a list of the vertebral counts of male and female plaice from the major areas. No significant difference was found between the male and female vertebral averages. The grand averages for males of 45.600 ± 0.011 and for females 45.619 ± 0.010 are not significantly different ($P = 0.20$).

It was generally not possible to compare averages of males and females from a single year-class in any one area because of the small sample size included. However, a comparison of vertebral averages for males and females of the 1952 year-class in St. Mary's Bay gives an average of 45.559 ± 0.072 for males and 45.658 ± 0.062 for females. These are not significantly different ($P = 0.30$). Thus, since no differences in vertebral averages are apparent between the sexes, the vertebral frequencies of male and female plaice have been combined in succeeding comparisons.

VERTEBRAL AVERAGES OF AMERICAN PLAICE FROM THE NORTHWEST ATLANTIC

The Overall Picture

In general the highest averages are found in the area extending from Hawke Channel southward over the entire Grand Bank, inshore to St. Mary's Bay and also to Banquereau. On the other hand the lowest averages occur in the Gulf of St. Lawrence, off Labrador and on Flemish Cap. Figure 2 shows the individual averages which are also listed in Appendix I. Figure 3 gives the averages and Table II the frequencies and related data for the combined samples.

An analysis of variance of both the individual samples and the vertebral frequencies for the various areas shows significant heterogeneity. (F for samples = 2.26 for $F_{05} = 1.28$, $F_{01} = 1.40$ and F for areas = 4.51 for $F_{05} = 1.57$, $F_{01} = 1.87$). Table II gives, in addition to the area frequencies and averages, the results of an analysis of variance of the samples within each area. One area, St. Pierre Bank, has a significant difference at the 1% level. The Hamilton Inlet Bank and Flemish Cap samples are significantly different at the 5% level. These areas are considered in a later section where the possible effect of combining samples over a number of years is discussed. The subdivision of the whole area into smaller areas has been mainly geographic, although in some cases the divisions were more or less arbitrary.

No statistically significant difference can be demonstrated between the vertebral samples from the area extending from Hawke Channel southward (excluding Notre Dame and White Bays) over the whole of the Grand Bank, and inshore to St. Mary's Bay and an area that can be referred to as the East Newfoundland Shelf ($F = 1.09$ for F_{05} of 1.90 and F_{01} of 2.50). The average for this area is 45.655 ± 0.009. If the samples from Hamilton Inlet Bank are included the average becomes 45.645 ± 0.009 ($F = 1.60$ for F_{05} of 1.35 and F_{01} of 1.52).

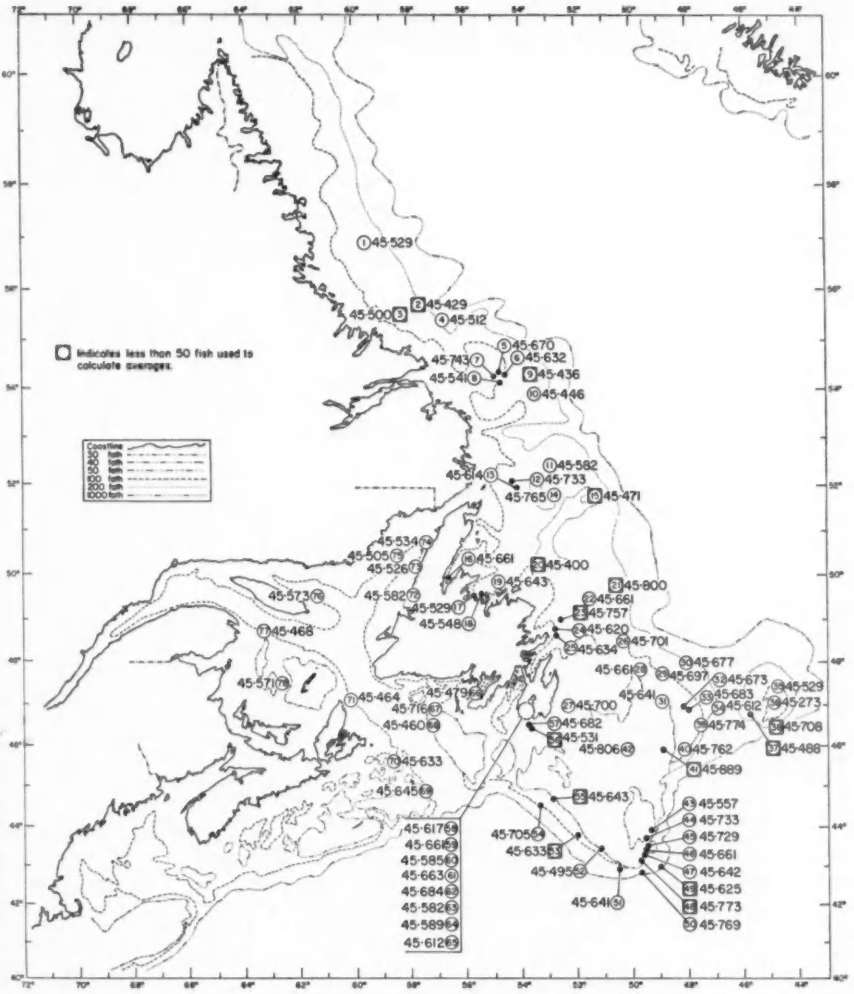


FIG. 2. Average vertebral number in American plaice samples. For details of samples see Appendix I.

The Labrador Shelf average (samples 1–4) is 45.511. It is not significantly different from the Hamilton Inlet Bank average (samples 5–10), 45.593 ($P = 0.08$), Notre Dame Bay, 45.551 ($P = 0.4$) and the Gulf of St. Lawrence, 45.512 ($P = 0.9$). It is significantly different from the Northeast Newfoundland Shelf average (samples 11–15), 45.634 ($P = 0.01$). The Hamilton Inlet Bank samples resemble some of the Labrador Shelf and some of the East Newfoundland Shelf samples, a point that will be brought out in the discussion of "period" differences. The average for White Bay (45.661) is comparatively high, and is similar to most

of the East Newfoundland Shelf samples. Notre Dame Bay is similar to the Northeast Newfoundland Shelf average (P = 0.07) but is significantly different from the Bonavista Shelf average 45.662 (P = 0.03).

All the averages from the Gulf of St. Lawrence are statistically similar (No. 71–78, Appendix 1), F = 1.13 for F_{05} of 3.23 and F_{01} of 5.67. The averages are generally low with the overall average being 45.512±0.017. This average is similar to that of the 1957 sample (No. 68) from St. Pierre Bank, 45.460 (P = 0.5), and to the Fortune Bay sample, 45.479 (P = 0.6). The Banquereau

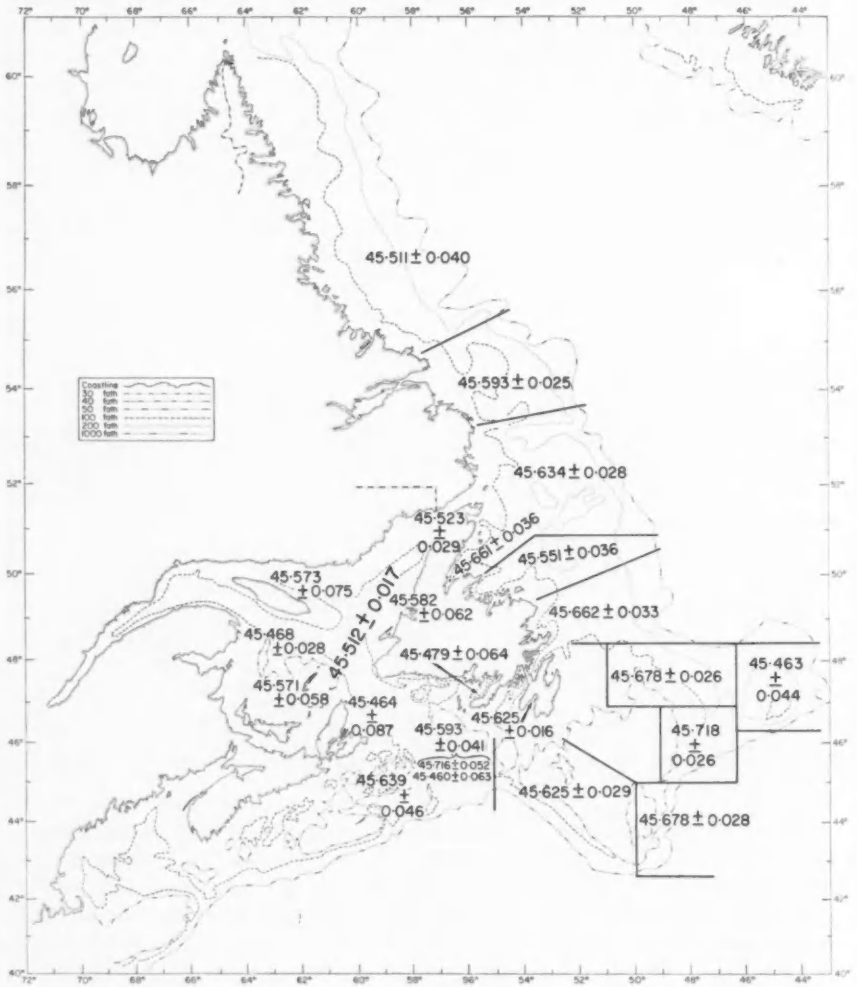


FIG. 3. Average vertebral number in American plaice samples combined by areas. For details see Table II.

TABLE II. Vertebral numbers of American plaice by areas and also an analysis of variance of the differences between the samples combined in the areas.

Area	Frequency											No. of samples	F Observed	F 5%	F 1%
	42	43	44	45	46	47	48	*N*	Mean	S_x	$S_{\bar{x}}$				
Labrador	...	...	13	113	128	10	...	264	45.511	0.652	0.040	4	7.29	8.54	26.19
Hamilton Inlet Bank	...	...	29	279	359	45	1	713	45.593	0.677	0.025	6	3.09	2.38*	3.34*
NE Nfld. Shelf	...	...	19	204	293	39	...	555	45.634	0.665	0.028	5	1.92	2.39	3.36
Notre Dame Bay	...	...	8	139	150	15	...	312	45.551	0.629	0.036	4	1.60	2.62	3.83
White Bay	...	...	2	41	66	6	...	115	45.661	0.605	0.056	1	...	...	...
Bonavista Shelf	...	...	10	142	210	28	1	391	45.662	0.659	0.033	5	1.49	5.64	13.48
N Grand Bank	...	...	29	231	388	57	2	707	45.678	0.694	0.026	6	1.03	4.37	9.04
NE Grand Bank	...	...	16	230	369	69	...	684	45.718	0.672	0.026	7	1.07	2.12	2.85
Flemish Cap	...	...	10	108	92	10	...	220	45.463	0.658	0.044	4	3.37	2.65*	3.88*
SE Grand Bank	1	...	12	204	320	41	2	580	45.678	0.666	0.028	8	1.15	2.03	2.69
SW Grand Bank	...	...	8	196	246	28	2	480	45.625	0.640	0.029	5	1.45	2.39	3.36
St. Mary's Bay	...	...	47	667	839	128	1	1,682	45.625	0.668	0.016	10	1.44	2.71	4.31
Fortune Bay	...	1	6	50	56	4	...	117	45.479	0.690	0.064	1	...	...	...
St. Pierre Bank	...	...	5	82	115	7	...	209	45.593	0.598	0.041	2	9.94	3.89*	6.76*
Port Saunders	...	...	15	214	224	19	...	472	45.523	0.628	0.029	3	1.62	19.50	99.50
Bonne Bay	...	...	3	47	53	7	...	110	45.582	0.655	0.062	1	...	...	...
N of Anticosti	...	...	2	42	38	6	1	89	45.573	0.705	0.075	1	...	...	...
Gaspé	...	...	18	249	223	16	...	506	45.468	0.620	0.028	1	...	...	...
Bradelle Bank	...	...	2	49	56	5	...	112	45.571	0.611	0.058	1	...	...	...
Off Cape North	...	...	4	34	26	5	...	69	45.464	0.719	0.087	1	...	...	...
Banquereau	...	...	6	86	108	19	...	219	45.639	0.679	0.046	2	0.017	254	6,366

*Significantly different.

average is significantly different from the combined Gulf average ($P = 0.003$) but is similar to the 1950 average (No. 67), 45.716, for St. Pierre Bank ($P = 0.3$). The latter average and those of Banquereau appear to be similar to those of the Grand Bank and in fact to most of the East Newfoundland Shelf.

The lowest average for the whole area was from Flemish Cap, with a sample taken in 1949 having an average of 45.273 (No. 36). The Flemish Cap average, 45.463, is significantly different from the 2 samples from neighbouring Grand Bank areas, the northern Grand Bank, 45.678 ($P = 0.001$) and the eastern Grand Bank, 45.718 ($P = 0.0001$). All the individual averages, for Flemish Cap, except No. 38 with 24 specimens, are significantly lower than those of the eastern and northeastern Grand Bank.

Meristic Characters and the Environment

Meristic characters are used to separate races or populations of a fish species on the theory that the hydrographic conditions during, and in some species apparently shortly following, incubation of the newly spawned egg cause variation in the number of certain parts of the fish such as the vertebrae, fin rays, gill rakers, etc. The extent of the variability is of course held within limits by the hereditary characteristics of the species. Temperature is apparently the environmental factor which has the most obvious influence on the determination of meristic characters in fish and many observations from nature point to a negative correlation between temperature and meristic number. Rounsefell and Dahlgren (1932) and Tester (1937) for the Pacific herring, *Clupea pallasi* Valenciennes, found a significant negative correlation between vertebral average and average air temperature during the spawning months. McHugh (1951) found a decrease in vertebral number from north to south on the Pacific Coast for the northern anchovy, *Engraulis mordax mordax* Girard. Many other workers have found similar negative correlations between vertebral number and temperature. However, for capelin, *Mallotus villosus* (Müller), Templeman (1948) found slightly higher vertebral averages in samples from the south coast of Newfoundland than for the more northerly east coast and Labrador; and Tibbo (1956) for the Atlantic herring, *Clupea harengus* L., in the Newfoundland area, found that there was a tendency for vertebral number to decrease with increasing latitude. Because the spawning period becomes progressively later from south to north, the more northerly fish develop in higher temperatures than those farther south due to the rise in inshore surface temperatures during the spring. The well-known experiments by Tåning (1944, 1952) with the sea trout, *Salmo trutta trutta* L., and other workers such as Gabriel (1944) with *Fundulus heteroclitus* (L.) and Dannevig (1950) with plaice, *Pleuronectes platessa* L., all suggest the probability that vertebral number is established quite early in the incubation of the fish egg. On the other hand, Lindsey (1954) working with the paradise fish, *Macropodus opercularis* L. was able to produce a change in vertebral number up to 11–12 days after hatching. Molander and Molander-Swedmark (1957) working with plaice, *Pleuronectes platessa* L., were also able to change the vertebral and fin ray numbers up to about 2 weeks after hatching.

TABLE III. Vertebral numbers of American plaice for certain areas to show possible "period" differences.

Area	Year	Sample No.	Vert. freq. 44	45	46	47	48	No. fish	Vert. av.	$S_{\bar{x}}$	S_x	
Hamilton Inlet Bank	1950	9	1	21	16	1	...	39	45.436	0.598	0.096	
" " "	1951	7	4	34	58	12	1	109	45.743	0.738	0.071	
" " "	1952	5	5	29	52	8	...	94	45.670	0.709	0.073	
" " "	1957	8	6	80	92	7	...	185	45.541	0.625	0.046	
" " "	1958	6	5	69	100	11	...	185	45.632	0.709	0.047	
" " "	1960	10	8	46	41	6	...	101	45.446	0.728	0.072	
NE Nfld. Shelf	1950	13 & 14	5	58	93	13	...	169	45.675	0.660	0.059	
" " "	1951	12	1	36	53	11	...	101	45.733	0.660	0.066	
" " "	1959	11	12	103	138	15	...	268	45.582	0.668	0.041	
NE Grand Bank	1949	31 & 39	8	76	132	21	...	237	45.700	0.688	0.044	
" " "	1950	33	1	48	59	12	...	120	45.683	0.661	0.060	
" " "	1958	32	5	71	103	17	...	196	45.673	0.668	0.048	
" " "	1961	30 & 34	10	75	127	15	1	228	45.658	0.670	0.045	
Flemish Cap	1949	36	6	38	20	2	...	66	45.273	0.669	0.082	
" "	1950	37	1	21	20	1	...	43	45.488	0.593	0.090	
" "	1961	35 & 38	3	49	52	7	...	111	45.568	0.655	0.062	
Hamilton Inlet Bank	1950–1952	...	10	84	126	21	1	242	45.665	0.711	0.046	P = >0.05
" " "	1957–1960	...	19	195	233	24	...	471	45.556	0.656	0.030	
NE Nfld. Shelf	1950 & 1951	...	6	94	146	24	...	270	45.696	0.660	0.040	P = >0.05
" " "	1959	...	12	103	138	15	...	268	45.582	0.668	0.041	
NE Grand Bank	1949 & 1950	...	9	124	191	33	...	357	45.695	0.700	0.035	P = 0.5
" " "	1958 & 1961	...	15	146	230	32	1	424	45.665	0.678	0.033	
Flemish Cap	1949–1950	...	7	59	40	3	...	109	45.358	0.646	0.062	P = 0.04
" "	1961	...	3	49	52	7	...	111	45.568	0.655	0.062	
St. Pierre Bank	1950	67	...	36	68	5	...	109	45.716	0.546	0.052	P = 0.02
" " "	1957	68	5	46	47	2	...	100	45.460	0.626	0.063	
Esquiman Channel	1950	75	1	54	43	5	...	103	45.505	0.608	0.059	P = 0.80
" "	1957	73	9	118	129	10	...	266	45.526	0.627	0.038	

The correlation of meristic numbers with other factors of the environment such as light, oxygen and carbon dioxide tension, pressure and salinity has been demonstrated sometimes under experimental conditions (Tåning, 1952), but has not been conclusively demonstrated in nature. Information on other environmental conditions is not readily available, so that only the relationship of American plaice vertebral numbers to temperature can be considered here.

COMPARISON OF SAMPLES TAKEN OVER AN EXTENDED PERIOD

The samples from the various areas were taken during the period 1949–1961. Actually the collection of samples occurred principally in 2 periods 1949–1952 and 1957–1961. Comparisons are possible in 6 areas only, and these are shown in Table III. The samples have been divided according to the 2 periods noted above.

HAMILTON INLET BANK. For this area the combined 1950–1952 average of 45.665, though somewhat higher than the 1957–1960 average of 45.556, is not significantly different from it (P slightly more than 0.05). For the individual averages, a significant difference at the 5% level was noted previously. This difference between individual averages can be attributed principally to the comparatively low average of the 1960 sample (No. 10) 45.446. This average is not only significantly lower than the early period averages (disregarding No. 9 with only 39 fish) but it also differs from the 1958 average (No. 6) of 45.632. The 1960 average, 45.446, and the 1957 average, 45.541, appear to be similar to those from the Labrador Shelf, most of which were taken in 1960, whereas the earlier averages are similar to those of the earlier period for the Northeast Newfoundland Shelf.

NORTHEAST NEWFOUNDLAND SHELF. Here, also, the 1950–1951 average 45.696 is not significantly different from the vertebral average, 45.582, of the sample taken in 1959 (P a little higher than 0.05).

NORTHEAST GRAND BANK. The 1949–1950 average, 45.695, is not significantly different from the 1958–1961 average, 45.665 (P = 0.5). The individual yearly averages are also similar regardless of whether they were taken during the early or more recent period.

FLEMISH CAP. The 1949–1950 average of 45.358 is significantly lower than the 1961 average of 45.568 (P = 0.04). This difference can be attributed to the very low 1949 average, 45.273.

ST. PIERRE BANK. There are 2 samples only, 1 in 1950 and the other in 1957. As Table III shows, the 1957 (45.460) average is significantly lower than the 1950 average (45.716) (P = 0.002). Figure 4 shows the year-class distribution of these 2 samples to be almost entirely different.

ESQUIMAN CHANNEL. The 1950 average, 45.505, and the 1957 average, 45.526, are not significantly different.

DISCUSSION

Within most areas a large number of year-classes have been included since most samples contain fish that could range in age from 4 up to possibly 25 years. The vertebral averages thus reflect not only the year to year temperature differ-

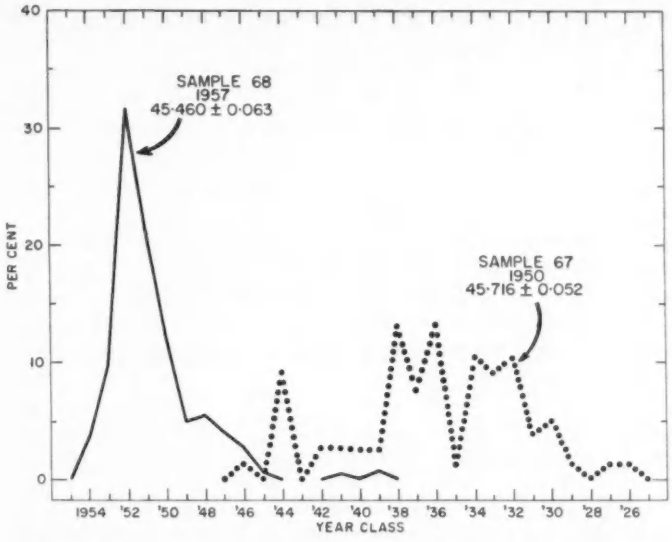


FIG. 4. Year-class frequency of St. Pierre Bank samples, Nos. 67 and 68.

ences, but also the possible gradual upward trend in the water temperatures for the Northwest Atlantic (Templeman and Fleming, 1953; Lauzier, 1954, 1958). The ideal way to treat this problem would be to compare fish of the same year-class from different areas. However, because of the large number of year-classes involved it has been usually impossible to secure enough fish of the various year-classes to make up reliable averages. A comparison of the vertebral numbers of individual year-classes of plaice within a single area, St. Mary's Bay, is presented in a later section.

The Hamilton Inlet Bank and Northeast Newfoundland Shelf data suggest the possibility that the more recent vertebral averages are lower than in earlier years, but the statistical evidence is not very conclusive. Farther south on the northeastern Grand Bank there has been no apparent change in the vertebral averages over a period of years. On the other hand the Flemish Cap averages are higher in more recent years.

With the small amount of variability between even the highest and lowest average for the whole area, 45.273 to 45.806 (for 30 fish or more), it is possible that 2 or 3 strong year-classes produced in a year with unusually high or low surface temperatures could result in a change in the usual vertebral average within any area. The Hamilton Inlet Bank area is apparently subject to considerable fluctuation in surface temperature and a later section will show that over a period of years July temperatures ranged from 1 to 8° C.

For St. Pierre Bank we have samples composed of almost entirely different year-classes and here again a change in surface temperatures for a few years could bring about a difference in vertebral number. In this case, however, the

more likely possibility is that St. Pierre Bank is stocked from 3 sources: the inshore area along the southwest coast, the eastern part of St. Pierre Bank and the northwest section of the Grand Bank, with the inshore area producing fish with the lowest count such as that recorded for Fortune Bay in 1952 (45.479).

In the Gulf of St. Lawrence there has been no apparent change in the vertebral averages. The Esquiman Channel samples for 1950 and 1957 are similar and over the whole of the Gulf the averages have remained consistently low although the samples were taken from 1949 to 1960.

The low degree of variability, plus the possible "period" changes for certain areas, makes the task of relating the vertebral averages to the general surface temperature picture of the area rather difficult. However, in the following sections an attempt is made to show why there is not a great variation between vertebral averages over the whole area and to give some indication of the probable origin of the stocks of plaice.

THE RELATIONSHIP OF AMERICAN PLAICE VERTEBRAL NUMBERS TO SURFACE TEMPERATURES IN THE NORTHWEST ATLANTIC

The exact time of spawning of American plaice in the Northwest Atlantic is not completely known but it varies considerably over the entire area. In addition, within any area some fish spawn long after the main spawning period, so that the presence of a few eggs late in the summer does not necessarily indicate a large-scale spawning. For St. Mary's Bay on the south coast of Newfoundland, the author has records showing that although the bulk of the spawning is usually completed early in May, a few fish were still extruding eggs well into June. It should also be remembered that there are probably yearly differences in the time of spawning which result from differences in bottom temperatures.

Table IV lists the probable spawning times of American plaice for the principal spawning areas of the Northwest Atlantic. For the more northerly areas especially, the dates are based on rather indirect evidence. No samples were secured from these areas before August, mainly because the presence of drift ice usually makes research cruises to these areas difficult until at least June or July. The estimate of the time of spawning has to be based on the relative amount of recovery of spent plaice taken in August from Hamilton Inlet Bank compared with those from areas where we have first-hand information of the exact spawning dates.

Frost (1938) found large numbers of American plaice eggs in the Strait of Belle Isle area in June and early July. For the southern part of the Gulf of St. Lawrence, Huntsman (1918) gives May and June as the spawning time of the American plaice and Powles (MS, 1959) confirms this. However, later information (Powles, personal communication) would indicate that spawning begins in mid April. In addition to the principal offshore spawning areas there are some plaice that spawn in the coastal waters of the northeast and east coasts of Newfoundland.

After the eggs are fertilized and development starts they float to the surface or perhaps remain just a little below it. Huntsman (1918) found in the waters

TABLE IV. Summary of spawning time, temperature and vertebral averages. (Vertebral averages used in the range are for samples of 20 fish or more.)

Area	Probable spawning time	Approx. surface temperature at spawning	Approx. surface temperature during early development	Vertebral number	
				Average	Range of averages
		°C	°C		
Labrador Shelf	June (?)	0 to −1 (?)	1 to 7 (July–August (?))	45.511	45.429–45.529
Hamilton Inlet Bank	June (?)	0 to −0.5	1 to 8 (July–August (?))	45.593	45.446–45.743
NE Nfld. Shelf	June (?)	0 to −0.5 (?)	?	45.634	45.582–45.765
White Bay	June (?)	0 (?)	?	45.661	...
Notre Dame Bay	June (?)	0 (?)	?	45.551	45.400–45.643
Bonavista Shelf	May (?)	0 to 2 (?)	?	45.662	45.620–45.800
NE Grand Bank	Mid April to mid May	0 to 3	3 to 5 + (May–June)	45.678	45.641–45.701
E Grand Bank	April	0 to 3		45.718	45.612–45.806
SE Grand Bank	April	0 to 3	3 to 5 + (May)	45.678	45.557–45.769
SW Grand Bank	March–April	1 to 4	3 to 6 (April–May)	45.625	45.495–45.705
Flemish Cap	April	3 to 6	6 to 8 (May)	45.463	45.273–45.529
St. Mary's Bay	April–May	0 to 4	3 to 5 + (May–June)	45.625	45.582–45.684
St. Pierre Bank	April–May	1 to 3	7 to 8 (June)	45.593	45.460 and 45.716
Fortune Bay	April–May	2 to 3	6 + (June)	45.479	
Gulf of St. Lawrence	Mid April to June	3 to 7[a]	4 to 8 (June) 12 to 17 (July)	45.512	45.464–45.582
Banquereau	Early April	1 to 4[b]	4 + (April–May)	45.639	45.633 and 45.645

[a]Lauzier *et al.* (1957).
[b]Hachey (1939, 1942).

between Cape Breton and the Magdalen Islands that the plaice eggs which were approaching the hatching stage were mainly at a depth of about 10 fathoms (18 m), whereas recently spawned eggs were nearer the surface. However, Dannevig (1919) found fairly large numbers of plaice eggs and also plaice larvae near the surface in the Gulf of St. Lawrence, off the east coast of Nova Scotia and south of Newfoundland.

Table IV also lists the probable surface temperatures to which the newly laid eggs are exposed when they come to the surface. Here again insufficient information is available on surface temperatures for the more northerly areas. With the amount of wave action usually prevalent in the Northwest Atlantic the upper 6–8 fathoms (10–15 m) probably have fairly uniform temperatures up to at least June (Lauzier *et al.*, 1957), so that when we refer to surface temperatures we include the upper 10–15 m. The Labrador Shelf and Northeast Newfoundland Shelf temperatures are based on 2 cruises of vessels operated by the St. John's Biological Station, one in 1958 (June 8–10) and the other in 1962 (May 31–June 1), both to the eastern part of Hamilton Inlet Bank. Surface temperatures in this area ranged from 0.2 to −0.5° C in 1958 and −0.3 to −0.4° C in 1962. The remaining temperatures, except where noted, are from information gathered on regular cruises of research vessels of the St. John's Station.

For most of the East Newfoundland Shelf there is probably not much difference in the surface temperature over the whole area when the eggs come to the surface, if we allow for later spawning in the more northerly areas, with the developing eggs being exposed to temperatures generally in the vicinity of 0 and 2° C. The southwest Grand Bank vertebral averages are a little higher and those of the Labrador Shelf a little lower than would be expected if we assume a negative correlation with temperature. However, the southwest Grand Bank population is not large and is probably derived from young plaice that migrate from the central part of the Grand Bank. Even without this possibility the range of 45.495–45.705 fits fairly well into the range of temperature conditions. The samples from the Labrador Shelf, on the other hand, have vertebral averages that are slightly lower than expected, but these were nearly all taken in a single cruise in 1960 (except for a sample of 21 fish in 1950) and thus late year-classes only are represented.

Flemish Cap and the Gulf of St. Lawrence both have comparatively high spring temperatures and both also have some of the lowest vertebral numbers recorded. In the latter area all vertebral averages were statistically similar indicating either that the larvae were subjected to similar temperature conditions or that the plaice in the Gulf have a common origin. Fortune Bay is represented by a single sample and the St. Pierre Bank vertebral average is made up of 2 samples caught in 1950 and 1957 that differ significantly and contained fish of almost entirely different year-classes, as previously noted. The Banquereau average is higher than would be expected for the usual spring temperatures, so it is possible that this area is stocked by larval drift from the southern part of St. Pierre Bank and Grand Bank.

If, however, we assume that the time when the vertebral number can be altered extends into the larval period (Molander and Molander-Swedmark, 1957) and for the moment we disregard larval drift, we have to deal with a different temperature picture. Hachey *et al.* (1954) give the approximate surface temperatures for Hamilton Inlet Bank in August 1950 as 6–8° C and similar temperatures were recorded Aug. 7–10, 1959 and Aug. 2–5, 1960 on cruises of the *A.T. Cameron*. However, on July 30–31, 1954 the surface temperature in this area was 1° C, so that the temperature range would be approximately 1–8° C. Table IV lists these probable temperatures and those of the whole area, but again we must note that the larvae may be below the surface and possibly thus subjected to slightly lower temperatures than those recorded. For the Grand Bank the upper range has perhaps been placed too low, but the average is probably close to the usual surface conditions for the periods in which the newly hatched larvae are pelagic. Generally, the temperatures to which the larvae of the whole east Newfoundland Shelf spawnings are exposed are fairly uniform if the lag in spawning from south to north is actually as great as Table IV shows. The high temperatures of the other areas (Gulf of St. Lawrence, Flemish Cap, St. Pierre Bank and Fortune Bay) would probably be expected to produce lower vertebral averages than those recorded, even allowing for the occasional "cold" year, if the number of vertebrae is determined during the early larval period.

THE RELATIONSHIP OF EGG AND LARVAL DRIFT TO VERTEBRAL NUMBERS

In trying to relate vertebral average to the surface temperatures of the area of capture there is always the possibility that the population owes its existence either entirely, or in part, to recruitment from other areas.

Preliminary information from tagging of American plaice by the St. John's Biological Station indicates that no extensive migrations of adult plaice occur. It therefore seems highly unlikely that migration will have any significant effect on the vertebral averages of the areas under consideration here.

According to Bigelow and Schroeder (1953) incubation occupies 11–14 days at about 4° C. Lower temperatures would extend this period. The larva drifts freely up to the time of its metamorphosis and sinks deeper as it grows, until it finally settles on the bottom. According to Bigelow and Schroeder (1953) the period occupied in larval growth and metamorphosis probably occupies 3–4 months in the Gulf of Maine. In most of the area covered by this paper the period of larval drift is probably longer because the lower temperatures would prolong the period occupied by larval growth and metamorphosis. The distance from the spawning ground to the place where the young plaice finally settle could thus be quite considerable.

The surface circulation in the Northwest Atlantic, being generally from north to south, would probably carry many eggs and larvae from spawnings in Labrador and the Northeast Newfoundland Shelf area toward the Grand Bank and it seems possible that the Grand Bank plaice population is in part derived from egg and larvae which have drifted from the more northerly areas and from along the

entire Newfoundland coast. Frost (1938) found early stage eggs and larvae in September 1932 over the northern part of the Grand Bank with their distribution continuous northward to the Straits of Belle Isle. These almost certainly came from either the northern area or from inshore spawning, because a spring cruise of the same year in May and early June produced abundant catches of plaice eggs and larvae over the Grand Bank but with very few to the north. This would seem to indicate an earlier spawning on the Grand Bank. It does not, however, seem likely that the entire Grand Bank population is recruited from the north as Frost (1938) suggests. The more logical explanation seems to be that although there is probably a high mortality by egg and larval drift beyond the continental shelf yet many are swept back by the eddying action at the edge of the bank.

Frost (1938) suggests that if most of the northern eggs and larvae are swept to the south then the Labrador and Hamilton Inlet Bank population is recruited either from migration from the south or by larval drift from West Greenland. However, while it is known that the latter area does support a plaice population there is, as yet, no evidence of larval drift of plaice from West Greenland. There is, however, strong evidence that the more northerly population of redfish, *Sebastes marinus mentella* Travin, of the Baffin Island–northern Labrador areas are recruited by larval drift by way of West Greenland (Templeman, 1959). In research cruises in 1959 and 1960 covering the continental shelf from off Cape Dyer to Hamilton Inlet Bank by the *A.T. Cameron* operated by the St. John's Biological Station of the Fisheries Research Board of Canada, a few plaice, some of which had previously spawned, were recorded in most localities. These records, while not indicating a large population in these northerly waters, do, however, provide a possible source of recruitment for the Labrador and Hamilton Inlet Bank populations.

In the northern half of the Gulf of St. Lawrence there is a movement of water into the Gulf on the north side of the Strait of Belle Isle and outward on the south side (Huntsman *et al.*, 1954). For the southern half of the Gulf the circulation is outward on the Cape Breton side and inward on the Newfoundland side of Cabot Strait (MacGregor, 1956). These movements obviously could result in both recruitment from Labrador and the south coast–St. Pierre Bank area and also loss of eggs and larvae by the outward movements from the Gulf. However, the central part of the Gulf of St. Lawrence has counterclockwise eddies which should help retain the larvae and also the fact that this area has consistently low vertebral averages suggests that it is likely to be self-sustaining.

VERTEBRAL NUMBERS OF AMERICAN PLAICE OF VARIOUS YEAR-CLASSES FROM ST. MARY'S BAY

Samples have been collected regularly from St. Mary's Bay for a number of years and in 1957 monthly samples were secured and vertebral counts done on all fish. This is the only area from which enough fish were secured within a limited period to give a good comparison of year-class vertebral averages.

For this comparison fish of ages 4–15 have been used, and the year-classes 1942 to 1953 have been considered (Table V). The analysis of variance shows

TABLE V. Vertebral frequencies of different year-classes of American plaice for St. Mary's Bay, Nfld.

Year-class	Frequency						N	Mean	$S_{\bar{x}}$	$S_{\bar{x}}$
	43	44	45	46	47	48				
1953	...	1	18	18	2	...	39	45.538	0.643	0.103
1952	...	7	82	102	16	...	207	45.614	0.679	0.047
1951	...	1	56	50	2	...	109	45.486	0.555	0.053
1950	...	3	59	62	8	1	133	45.586	0.675	0.059
1949	...	1	27	23	5	...	56	45.571	0.684	0.091
1948	...	1	41	54	12	...	108	45.713	0.671	0.065
1947	...	2	26	44	11	...	83	45.771	0.704	0.077
1946	...	4	62	87	12	...	165	45.648	0.651	0.051
1945	...	2	20	35	5	...	62	45.694	0.668	0.085
1944	...	4	39	44	5	...	92	45.543	0.670	0.070
1943	...	1	31	41	6	...	79	45.658	0.638	0.072
1942	...	1	21	29	7	...	58	45.724	0.696	0.091

no significant difference at the 5% level. ($F = 1.44$ for $F_{05} = 1.80$ and $F_{01} = 2.26$.)

A positive correlation has been found to exist between air and surface-water temperatures (Rounsefell and Dahlgren, 1932; Templeman and Fleming, 1953) but since no surface temperatures are available the air temperatures from a nearby coastal reporting station (Cape Race) can be used for comparison. In order to see if a correlation exists between temperature and vertebral averages the latter have been compared with the calculated average air temperatures during the early spring. Table VI lists the vertebral averages for year-classes of 1942–1953 with the mean air temperatures for March–April and April–May. The correlation coefficient (r) is –0.521 for March–April and –0.503 for April–May. The P-values are 0.05 and 0.10, respectively, indicating that the correlations are not good. Part of the failure to find a good relationship between the mean number of vertebrae and air temperature during the spawning period can perhaps be attributed to the smallness of the samples and the possibility of some fish being placed in the wrong year-class through errors in ageing. However, the most serious difficulty in correlating vertebral average with air temperature, and thus we presume surface temperature, is that there may be in certain years a delay in the time of spawning, with the latter being influenced by bottom temperatures which are in turn determined in this case by the Labrador Current and not by surface temperature penetration. For example, in a year when the volume of the Labrador Current entering St. Mary's Bay was great, spawning could be delayed with the eggs coming to the surface toward the middle of May, whereas in an early spawning year the eggs could be exposed to middle-of-April temperatures. It is obvious that unless we are sure of the spawning time we cannot be sure of which air temperature to use in correlating vertebral count.

TABLE VI. Vertebral averages for the 1942–1953 year-classes from St. Mary's Bay compared with the average air temperatures at Cape Race, Nfld.

Average air temp. March–April	Vert. av.	Year-class	Average air temp. April–May	Vert. av.	Year-class
°C	A		°C	B	
−3.1	45.713	'48	1.4	45.571	'49
−1.4	45.586	'50	1.5	45.771	'47
−1.2	45.771	'47	1.6	45.713	'48
−1.2	45.543	'44	2.1	45.543	'44
−0.9	45.694	'45	2.2	45.694	'45
−0.8	45.658	'43	2.6	45.648	'46
−0.3	45.648	'46	2.6	45.658	'43
0.2	45.538	'53	3.0	45.586	'50
0.4	45.724	'42	3.3	45.614	'52
0.6	45.571	'49	3.5	45.724	'42
0.7	45.614	'52	3.7	45.538	'53
1.7	45.482	'51	4.4	45.482	'51

GENERAL DISCUSSION AND CONCLUSIONS

In explaining the low degree of variability of American plaice vertebral averages for the Northwest Atlantic several possibilities can be put forward.

(a) The genetic character of American plaice may be such that the variability of the meristic parts is not highly influenced by the external environment.

(b) Factors of the environment other than temperature may complicate the usual relationship of high temperature–low vertebral number and vice versa. This, however, is considered to be improbable.

(c) The probable differences in the spawning time for various localities may result in the developing eggs and/or early larvae being subjected to essentially similar hydrographic conditions.

(d) If the inherent variability is only slight, the yearly fluctuations in temperature in a particular area may be reflected in the vertebral number for the different year-classes and thus years with high sea temperatures in the upper layers would produce fish with low vertebral number but in cold years the opposite would happen, thus counterbalancing each other. High bottom temperatures could cause early spawning with the eggs rising to the surface before the upper layer had warmed up. The opposite could happen in a year that the bottom temperatures were low, with the delay in spawning causing the newly-spawned eggs to rise to the surface and develop in surface layers that had warmed up. This applies especially to areas that come under the influence of the Labrador Current. Its probable effect in influencing the year-class averages from St. Mary's Bay has already been noted.

In the commercial fishing areas of the Grand Bank, vertebral averages of American plaice do not demonstrate the existence of separate populations. On the other hand, information from tagging and age–length data, as yet unpublished, suggest that the Grand Bank adult population can be divided into fairly discrete populations. In the Gulf of St. Lawrence the persistently low vertebral averages for the various sections of the Gulf, coupled with the high spring temperatures, strongly suggest that the population of American plaice in this area is self-sustaining.

ACKNOWLEDGMENTS

The author is especially grateful to Dr W. Templeman, Director of the Fisheries Research Board of Canada Biological Station, St. John's, Newfoundland, for his suggestions and criticisms in the preparation of this paper, and also to Mr C. A. Rose who assisted especially in age readings and in the various statistical calculations and to the many members of the staff of the Station who were involved in the collection and preparation of the original data for this paper. I also wish to thank Mr V. M. Hodder for helpful suggestions and also other colleagues for critical reading of the original manuscript.

REFERENCES

BIGELOW, HENRY B., AND WILLIAM C. SCHROEDER. 1953. Fishes of the Gulf of Maine. *U.S. Fish and Wildlife Serv. Bull.*, **53**(74): 1–577.

DANNEVIG, ALF. 1919. Canadian fish-eggs and larvae. Canadian Fish. Exped., 1914–15, pp. 1–74, Ottawa.

1950. The influence of the environment on the number of vertebrae in plaice. *Rep. Norwegian Fish. and Mar. Inv.*, **9**(9): 1–6.

FROST, NANCY. 1938. Some fishes of Newfoundland waters. *Dept. Natural Resources, Newfoundland Res. Bull.*, No. 4, 16 pp.

GABRIEL, M. L. 1944. Factors affecting the number and form of vertebrae in *Fundulus heteroclitus* (L.). *J. Exp. Zool.*, **95**: 105–143.

HACHEY, H. B. 1939. Surface water temperatures of the Canadian Atlantic coast. *J. Fish. Res. Bd. Canada*, **4**(5): 378–391.

1942. The waters of the Scotian Shelf. *Ibid.*, **5**(4): 377–397.

HACHEY, H. B., F. HERMANN AND W. B. BAILEY. 1954. The waters of the ICNAF convention area. *Int. Comm. NW Atlantic Fish., Ann. Proc.*, **4**: 67–102.

HUNTSMAN, A. G. 1918. Histories of new food fishes. 1. The Canadian plaice. *Bull. Biol. Bd. Canada*, No. 1, 32 pp.

HUNTSMAN, A. G., W. B. BAILEY AND H. B. HACHEY. 1954. The general oceanography of the Strait of Belle Isle. *J. Fish. Res. Bd. Canada*, **11**(3): 198–260.

LAUZIER, L. 1954. Recent surface water temperatures along the Canadian Atlantic coast. Cold years — warm years. *Fish. Res. Bd. Canada, Atlantic Prog. Rept.*, No. 58, pp. 6–10.

1958. Surface sea water temperatures along the Canadian Atlantic coast, 1954–1957. *Ibid.*, No. 71, pp. 8–12.

LAUZIER, L., R. W. TRITES AND H. B. HACHEY. 1957. Some features of the surface layer of the Gulf of St. Lawrence. *Bull. Fish. Res. Bd. Canada*, No. 111, pp. 195–212.

LINDSEY, C. C. 1954. Temperature-controlled meristic variation in the paradise fish, *Macropodus opercularis* (L.). *Canadian J. Zool.*, **32**: 87–98.

MACGREGOR, D. G. 1956. Currents and transport in Cabot Strait. *J. Fish. Res. Bd. Canada*, **13**(3): 435–448.

MCHUGH, J. L. 1951. Meristic variations and populations of northern anchovy (*Engraulis mordax mordax*). *Bull. Scripps Inst. Oceanog. Univ. California*, **8**(3): 123–160.

MOLANDER, ARVID R., AND MARTHA MOLANDER-SWEDMARK. 1957. Experimental investigations on variation in plaice (*Pleuronectes platessa* Linné). *Rep. Inst. Mar. Res., Lysekil, Ser. Biol.*, No. 7, 44 pp.

POWLES, P. M. MS, 1959. Plaice studies. *Fish. Res. Bd. Canada, Ann. Rept. Atlantic Biol. Sta.* for 1958–59 (mimeographed), App. No. 31, pp. 56–58.

ROUNSEFELL, GEORGE A., AND EDWIN H. DAHLGREN. 1932. Fluctuations in the supply of herring, *Clupea pallasii* in Prince William Sound, Alaska. *Bull. U.S. Bur. Fish.*, **47**: 262–291. (Bull. No. 9)

TÅNING, Å. VEDEL. 1944. Experiments on meristic and other characters in fishes. 1. On the influence of temperature on some meristic characters in sea trout and the fixation-period of these characters. *Medd. Komm. Danmarks Fiskeri-og Havunders., Fiskeri*, **11**(3): 1–66.

1952. Experimental study of meristic characters in fishes. *Biol. Rev.*, **27**: 169–193.

TEMPLEMAN, WILFRED. 1948. The life history of the caplin (*Mallotus villosus* O. F. Müller) in Newfoundland waters. *Bull. Newfoundland Govt. Lab., Res. Ser.*, No. 17, 115 pp.

1959. Redfish distribution off Baffin Island, northern Labrador and in Ungava Bay in August-September 1959. *Int. Comm. NW Atlantic Fish. Special Publication* (*ICES/ICNAF Redfish Symposium*) No. 3, pp. 157–162. (Also in *Conseil Expl. Mer, Rapp. et Proc.-Verb.*, **150**: 157–162.)

TEMPLEMAN, WILFRED, AND A. M. FLEMING. 1953. Long term changes in hydrographic conditions and corresponding changes in the abundance of marine animals. *Int. Comm. NW Atlantic Fish., Ann. Proc.*, **3**: 79–86.

TESTER, ALBERT L. 1937. Populations of herring (*Clupea pallasii*) in the coastal waters of British Columbia. *J. Biol. Bd. Canada*, **3**(2): 108–144.

TIBBO, S. N. 1956. Populations of herring (*Clupea harengus* L.) in Newfoundland waters. *J. Fish. Res. Bd. Canada*, **13**(4): 449–466.

APPENDIX I.

American plaice vertebral statistics.

Sample No.	Year	Month	Locality	Position		Depth		Bottom temp.	Vertebral frequencies							Total fish	Vert. average	Stand. deviat.	Stand. error
				Lat.	Long.				42	43	44	45	46	47	48				
						fath	*m*	°C	%	%	%	%	%	%	%				
1	1960	Aug. 1	Labrador Shelf	56°56'N	59°36'W	99–126	181–230	−0.33	..	..	5.8	40.4	49.0	4.8	..	104	45.529	0.682	0.067
2	1950	Aug. 31	Labrador Shelf	55°44'N	57°34'W	120–124	220–227	0.23	..	..	4.8	52.4	38.1	4.8	..	21	45.429	0.676	0.148
3	1960	Aug. 2	Labrador Shelf	55°29'N	58°05'W	78	143	−0.62	..	..	8.3	33.3	58.3	..	..	12	45.500	0.674	0.199
4	1960	Aug. 5	Labrador Shelf	55°27'N	56°44'W	99–126	181–230	−0.70	..	..	3.9	44.1	48.8	3.1	..	127	45.512	0.628	0.056
5	1952	Sept. 21	Hamilton Inlet Bank	54°21'N	54°35'W	100	183	−0.28	..	..	5.3	30.9	55.3	8.5	..	94	45.670	0.709	0.073
6	1958	Aug. 7	Hamilton Inlet Bank	54°24'N	54°34'W	106–108	194–198	0.22	..	..	2.7	37.3	54.1	5.9	..	185	45.632	0.638	0.047
7	1951	Sept. 18	Hamilton Inlet Bank	54°17'N	54°55'W	100–94	183–172	0.12	..	..	3.7	31.2	53.2	11.0	0.9	109	45.743	0.738	0.071
8	1957	Aug. 9	Hamilton Inlet Bank	54°13'N	54°45'W	98–100	179–183	−0.23	..	..	3.2	43.2	49.7	3.8	..	185	45.541	0.625	0.046
9	1950	Sept. 6	Hamilton Inlet Bank	54°18'N	53°40'W	120–140	220–256	1.50	..	..	2.6	53.8	41.0	2.6	..	39	45.436	0.598	0.096
10	1960	Aug. 10	Hamilton Inlet Bank	53°55'N	53°07'W	88–102	161–187	0.62	..	..	7.9	45.5	40.6	5.9	..	101	45.446	0.728	0.072
11	1959	Sep. 29	NE Nfld. Shelf	52°26'N	52°57'W	127	232	0.71	..	..	4.5	38.4	51.5	5.6	..	268	45.582	0.668	0.041
12	1951	Sep. 24	NE Nfld. Shelf	52°06'N	54°20'W	106–104	194–190	0.84	..	..	1.0	35.6	52.5	10.9	..	101	45.733	0.662	0.066
13	1950	Sep. 28	NE Nfld. Shelf	51°56'N	54°08'W	138–140	252–256	1.29	..	..	3.0	39.6	50.5	6.9	..	101	45.614	0.663	0.066
14	1950	Sep. 25–27	NE Nfld. Shelf	51°49'N	52°45'W	157–230	287–420	2.46	..	..	2.9	26.5	61.8	8.8	..	68	45.765	0.649	0.079
15	1950	Sep. 24	NE Nfld. Shelf	51°48'N	51°19'W	176–195	322–357	2.38	..	..	5.9	41.2	52.9	..	..	17	45.471	0.624	0.151
16	1951	Oct. 8	White Bay	49°54'N	56°30'W	140	256	−0.65	..	..	1.7	35.7	57.4	5.2	..	115	45.661	0.605	0.056
17	1951	Nov. 1	Badger Bay	49°25'N	55°39'W	148–164	271–300	0.12	..	..	1.2	47.1	49.4	2.4	..	85	45.529	0.569	0.062
18	1951	Nov. 2	Notre Dame Bay	49°34'N	55°21'W	130–175	238–320	−0.70	..	..	2.4	44.0	50.0	3.6	..	84	45.548	0.609	0.066
19	1951	Nov. 14	Notre Dame Bay	49°47'N	54°51'W	80–196	146–358	0.28	..	..	2.0	40.8	48.0	9.2	..	98	45.643	0.677	0.068
20	1952	Sep. 4	Funk Island	50°00'N	53°58'W	148–212	271–388	2.05	..	..	6.7	48.9	42.2	2.2	..	45	45.400	0.654	0.097
21	1950	Jul. 25	Off Cape Bonavista	47°48'N	50°33'W	177–178	324–326	3.36	..	..	..	30.0	60.0	10.0	..	30	45.800	0.610	0.111
22	1950	Jul. 26	NE of Cape Bonavista	49°28'N	51°31'W	156–176	285–322	2.93	..	..	2.6	35.7	54.8	7.0	..	115	45.661	0.647	0.060
23	1950	Jul. 27	NE of Cape Bonavista	48°53'N	52°32'W	170–181	311–331	2.05	..	..	..	35.1	54.1	10.8	..	37	45.757	0.641	0.105
24	1951	Nov. 16	NE of Cape Bonavista	48°48'N	52°43'W	114–120	209–220	−0.97	..	..	3.7	38.0	50.9	7.4	..	108	45.620	0.680	0.065
25	1950	Jun. 30–Jul. 5	Cape Bonavista	48°30'N	54°40'W	No record	..	No record	..	..	3.0	37.6	53.5	5.0	1.0	101	45.634	0.674	0.067
26	1949	Oct. 5	N Grand Bank	48°30'N	50°15'W	82–122	150–223	1.10	..	..	3.7	31.8	55.1	9.3	..	107	45.701	0.690	0.067
27	1951	Apr. 17	Woolfall Bank	46°59'N	52°16'W	69–77	126–141	−0.77	..	..	4.5	30.0	56.4	9.1	..	110	45.700	0.698	0.067

APPENDIX I. (continued)

Sample No.	Year	Month	Locality	Position		Depth		Bottom temp.	Vertebral frequencies							Total fish	Vert. average	Stand. deviat.	Stand. error
				Lat.	Long.				42	43	44	45	46	47	48				
						fath	*m*	°C	%	%	%	%	%	%	%				
28	1954	Oct. 10	N Grand Bank	47°49'N	49°40'W	80–78	146–143	–0.81	..	..	4.6	34.9	51.4	8.3	0.9	109	45.661	0.736	0.070
29	1945	Sep. 20	N Grand Bank	47°48'N	48°49'W	122–125	223–229	0.28	..	..	3.4	32.6	55.1	9.0	..	89	45.697	0.681	0.072
30	1961	Mar. 28–29	NE Grand Bank	47°53'N	48°47'W	100–175	183–320	–0.49	..	..	3.7	32.9	55.9	6.8	0.6	161	45.677	0.686	0.054
31	1949	Aug. 5–6	NE Grand Bank	47°10'N	48°50'W	46–50	84–91	–0.21	..	..	4.6	33.6	55.0	6.9	..	131	45.641	0.680	0.059
32	1958	Jul. 18	NE Grand Bank	46°58'N	48°04'W	70–84	128–154	No record	..	..	2.6	36.2	52.6	8.7	..	195	45.673	0.668	0.048
33	1950	Jun. 16	NE Grand Bank	46°52'N	48°00'W	70	128	–1.06	..	..	0.8	40.0	49.2	10.0	..	120	45.683	0.661	0.060
34	1961	Mar. 26	NE Grand Bank	47°06'N	47°03'W	140–190	256–348	3.60	..	..	6.0	32.8	55.2	6.0	..	67	45.612	0.695	0.085
35	1961	Mar. 20–22	N of Flemish Cap	47°27'N	44°42'W	80–175	146–320	3.95	..	..	1.1	48.3	47.1	3.4	..	87	45.529	0.587	0.063
36	1949	Aug. 28–31	Flemish Cap	47°05'N	44°56'W	80–110	146–201	3.79	..	..	9.1	57.6	30.3	3.0	..	66	45.273	0.669	0.082
37	1950	Jul. 16	W of Flemish Cap	46°48'N	45°43'W	120–148	220–271	3.28	..	..	2.3	48.8	46.5	2.3	..	43	45.488	0.593	0.090
38	1961	Mar. 23	S of Flemish Cap	46°35'N	44°51'W	150	274	3.78	..	..	8.3	29.2	45.8	16.7	..	24	45.708	0.859	0.175
39	1949	Sep. 9	NE Grand Bank	46°35'N	47°32'W	86–90	157–165	0.62	..	..	1.9	30.2	56.6	11.3	..	106	45.774	0.666	0.065
40	1950	Aug. 17–19	E Grand Bank	45°55'N	48°05'W	98–100	180–185	No record	..	..	1.0	31.4	58.1	9.5	..	105	45.762	0.628	0.061
41	1949	Jul. 25	E Grand Bank	45°54'N	48°53'W	42	77	–0.20	..	..	..	33.3	44.4	22.2	..	18	45.889	0.758	0.179
42	1951	Apr. 13	Central Grand Bank	45°54'N	50°15'W	38–42	70–77	0.60	..	..	4.2	25.0	56.9	13.9	..	72	45.806	0.725	0.085
43	1951	Apr. 25	SE Grand Bank	43°52'N	49°20'W	36–44	66–81	No record	..	..	2.6	41.7	53.0	2.6	..	115	45.557	0.595	0.055
44	1950	Oct. 7–9	SE Shoal Grand Bank	43°40'N	49°32'W	30–70	55–128	" "	..	..	5.0	31.7	50.0	11.7	1.7	60	45.733	0.800	0.103
45	1950	Sep. 1–5	SE Grand Bank	43°30'N	49°25'W	48–80	89–146	" "	..	..	1.7	32.2	57.6	8.5	..	59	45.729	0.639	0.083
46	1950	Sep. 21–23	SE Grand Bank	43°25'N	49°32'W	40–85	73–155	" "	..	..	1.8	35.7	57.1	5.4	..	56	45.661	0.611	0.082
47	1949	Aug. 17	SE Grand Bank	43°15'N	49°34'W	40–80	73–146	–0.65	..	..	0.9	39.6	53.8	5.7	..	106	45.642	0.605	0.059
48	1949	Nov. 10	SE Grand Bank	43°08'N	49°46'W	80–90	146–165	No record	..	..	..	34.1	56.8	6.8	2.3	44	45.773	0.677	0.102
49	1950	Oct. 8–12	SE Grand Bank	42°58'N	49°00'W	38–195	70–357	" "	..	..	3.1	37.5	53.1	6.3	..	32	45.625	0.660	0.117
50	1949	Dec. 11	SE Grand Bank	42°50'N	49°45'W	45	82	" "	0.9	..	1.9	26.9	59.3	11.1	..	108	45.769	0.744	0.072
51	1957	Jun. 13	S Grand Bank	42°54'N	50°28'W	80–81	146–148	" "	..	..	2.3	38.6	52.3	6.4	0.5	220	45.641	0.657	0.044
52	1950	Apr. 22	SW Grand Bank	43°24'N	51°07'W	60–86	110–157	–0.30	..	..	2.1	53.6	37.1	7.2	..	97	45.495	0.663	0.067
53	1953	Mar. 24	SW Grand Bank	43°45'N	52°00'W	65–75	119–137	No record	..	..	3.3	30.0	66.7	..	..	30	45.633	0.556	0.102
54	1950	Feb. 6	SW Grand Bank	44°30'N	53°16'W	65–73	119–134	" "	..	..	..	38.1	54.3	6.7	1.0	105	45.705	0.634	0.062
55	1950	Mar. 31	SW Grand Bank	44°39'N	52°50'W	54	99	" "	..	..	..	35.7	64.3	..	..	28	45.643	0.488	0.092

APPENDIX I. (concluded)

Sample No.	Year	Month	Locality	Position		Depth		Bottom temp.	Vertebral frequencies							Total fish	Vert. average	Stand. deviat.	Stand. error
				Lat.	Long.				42	43	44	45	46	47	48				
						fath	*m*	°C	%	%	%	%	%	%	%				
56	1949	Nov. 6	Off Cape Pine	46°28'N	53°42'W	47–52	86–95	1.01 av.	..	..	6.3	37.5	53.1	3.1	..	32	45.531	0.671	0.119
57	1949	Oct. 10	Off Cape Pine	46°30'N	53°45'W	33–38	60–70	No record	..	..	2.7	38.2	47.3	11.8	..	110	45.682	0.716	0.068
58	1957	Feb. 26	St. Mary's Bay	46°52'N	53°46'W	82–76	150–139	" "	..	..	3.2	37.8	53.2	5.9	..	222	45.617	0.647	0.043
59	1957	Apr. 9	St. Mary's Bay	46°51'N	53°50'W	71–72	130–132	" "	..	..	1.1	38.9	52.8	7.2	..	180	45.661	0.627	0.047
60	1957	May 29	St. Mary's Bay	46°50'N	53°50'W	70–68	128–124	−0.64	..	..	0.5	50.3	39.5	9.7	..	195	45.585	0.671	0.048
61	1957	Jun. 29	St. Mary's Bay	46°48'N	53°51'W	68	124	No record	..	..	3.9	33.7	54.7	7.7	..	181	45.663	0.676	0.050
62	1957	Aug. 3	St. Mary's Bay	46°51'N	53°49'W	46–47	84–86	" "	..	..	3.2	33.2	56.3	6.8	0.5	190	45.684	0.671	0.049
63	1957	Sep. 7	St. Mary's Bay	46°49'N	53°47'W	72–80	132–146	" "	..	..	3.3	43.8	44.4	8.5	..	153	45.582	0.694	0.056
64	1957	Oct. 5	St. Mary's Bay	46°50'N	53°48'W	80–82	146–150	" "	..	..	3.9	40.7	47.9	7.5	..	280	45.589	0.687	0.041
65	1957	Dec. 11	St. Mary's Bay	46°50'N	53°47'W	80–82	146–150	0 10	..	..	2.2	40.3	51.8	5.8	..	139	45.612	0.621	0.053
66	1952	Dec. 6	Fortune Bay	47°16'N	55°40'W	100–102	183–187	0.80	..	0.9	5.1	42.7	47.9	3.4	..	117	45.479	0.690	0.064
67	1950	Mar. 25–26	St. Pierre Bank	46°50'N	57°03'W	95–110	174–201	3.41	..	..	..	33.0	62.4	4.6	..	109	45.716	0.546	0.052
68	1957	Jun. 30	St. Pierre Bank	46°30'N	57°24'W	61–60	112–110	−0.13	..	..	6.0	46.0	47.0	2.0	..	100	45.460	0.626	0.063
69	1950	May 15	Banquereau	44°50'N	57°28'W	34–48	62–88	0.13	..	..	0.8	43.0	47.1	9.1	..	121	45.645	0.657	0.060
70	1952	Nov. 8	Off Cape Breton	45°35'N	58°30'W	50–100	91–183	3.08	..	..	5.1	34.7	52.0	8.2	..	98	45.633	0.709	0.072
71	1952	Nov. 2	Off Cape North	47°04'N	60°14'W	82–85	150–155	3.71	..	..	5.8	49.3	37.7	7.2	..	69	45.464	0.719	0.087
72	1950	Dec. 3	Bonne Bay	49°35'N	58°00'W	60–56	110–102	0.99	..	..	2.7	42.7	48.2	6.4	..	110	45.582	0.655	0.062
73	1957	Nov. 17	Esquiman Channel	50°18'N	57°43'W	100	183	3.04	..	..	3.4	44.4	48.5	3.8	..	266	45.526	0.627	0.049
74	1949	Nov. 22	Off Port Saunders	50°44'N	57°24'W	78–135	143–247	4.00	..	..	4.9	40.8	50.5	3.9	..	103	45.534	0.654	0.064
75	1950	Oct. 19	Esquiman Channel	50°28'N	58°29'W	80–120	146–220	2.12	..	..	1.0	52.4	41.7	4.9	..	103	45.505	0.608	0.059
76	1960	Nov. 12–13	N of Anticosti	49°25'N	61°30'W	100–122	183–223	4.07	..	..	2.2	47.2	42.7	6.7	1.1	89	45.573	0.705	0.075
77	1960	Nov. 15	Gaspé Area	45°38'N	63°16'W	100–200	183–366	4.35	..	..	3.6	49.2	44.1	3.2	..	506	45.468	0.620	0.028
78	1950	Nov. 10	Bradelle Bank	47°30'N	62°34'W	38	70	0.04	..	..	1.8	43.8	50.0	4.5	..	112	45.571	0.611	0.058

Brine Spray Frozen Tuna. Sodium, Potassium, Lactic Acid and Acid-Soluble Phosphorus in the Muscle, and the Influence Thereon of Thawing and Precooking[1]

By N. Tomlinson and S. E. Geiger

Fisheries Research Board of Canada
Technological Research Laboratory, Vancouver, B.C.

ABSTRACT

Analyses have been made for several soluble components of the white muscle from three species (albacore, bluefin and skipjack) of brine-spray frozen tuna. Fish from three different landings were examined. Penetration of sodium into the outer layers of muscle during freezing was quite high, but was negligible into the inner layers. Inorganic phosphate accounted for 80–85% of the total muscle acid-soluble phosphorus, indicating that extensive degradation of this fraction had occurred. The lactic acid content of the muscle was high in all species, ranging from 0.6 to 1.7%. Water-thawing of the frozen fish reduced the sodium content of the outer ½ inch of muscle by about 50% but had little effect on that of the underlying muscle. Cooking the fish did not have any clearly noticeable effect on the distribution of the soluble components in them. In practice, it has been found that the sodium content of the fish after water-thawing is acceptable for canning when a suitable reduction in the salt added is made to compensate for that present in their muscle.

INTRODUCTION

Recently, research has been undertaken in this Laboratory with the object of developing a procedure for freezing fish at sea suitable for use in a tuna fishery based in British Columbia. The fishing vessels being used are equipped with a brine-spray freezing system designed by the engineering section of the Laboratory (Roach and Harrison, 1963). Several landings of fish have been made, and the fish have been judged to be in excellent condition. Samples of fish from three of these landings have been analyzed chemically for a number of components (e.g. sodium and potassium), and the influence of thawing and precooking the fish on the concentration of these components in the muscle has been investigated.

METHODS AND MATERIALS

Three species of tuna have been examined; albacore (*Thunnus alalunga*), bluefin (*Thunnus saliens*) and skipjack (*Katsuwonus pelamis*). The albacore and bluefin weighed 14–18 lb each, while the skipjack weighed about 7 lb. Their stomach contents indicated all were feeding heavily prior to capture. After being frozen, the fish had been held at −4 to −7°C on the fishing vessels for about 4 weeks prior to landing, had been partially thawed to facilitate unloading and then transported to the Laboratory and held at −25°C for 1 or 2 weeks before being analyzed.

[1]Received for publication February 27, 1963.

J. Fish. Res. Bd. Canada, 20(5), 1963.
Printed in Canada.

Samples were taken from the white lateral-dorsal muscle in the region below the dorsal fin. Separate samples (5 g each) were taken from the first $\frac{1}{8}$ inch of muscle beneath the skin (including the fatty layer), from the next $\frac{1}{4}$ inch of muscle, and from the deep muscle near the backbone. Extraction of samples and methods of analysis of the extracts for sodium, potassium, lactic acid, and various acid soluble phosphorus fractions have been described previously (Tomlinson *et al.*, 1961, 1962). Muscle pH was determined using the method of Partmann (1960), and its "ultimate pH" by the method of Callow (1938). In Partmann's procedure, 2 g of muscle were homogenized at 0°C in 20 ml of 0.005*M* sodium iodoacetate solution and the pH of the homogenate was measured at once. In Callow's procedure, 10 g of muscle with 2 drops of chloroform added was homogenized in 20 ml of distilled water. The homogenate was held at room temperature for 1 hour and its pH was then taken. Measurement of pH was made with a Beckman model G pH meter. The samples of muscle from the first $\frac{1}{8}$ inch beneath the skin were analyzed for sodium and potassium only.

RESULTS AND DISCUSSION

The results of the analyses for various components of muscle samples from 3 species in one landing are listed in Table I. Penetration of sodium into the outer $\frac{1}{8}$ inch of muscle during freezing was quite high, but, while variable, was less into the next $\frac{1}{4}$ inch, and was negligible into the inner layers. There appears to have been some loss of potassium from the outer layers.

Lactic acid content of the muscle was high for each of the three species, ranging from 1.3 to 1.7% in the inner layer of muscle, and from 0.63 to 0.97% (with a single value of 1.5%) in the outer layer. The pH of the muscle ranged from 5.4 to 5.5 for skipjack and from 5.6 to 5.8 for albacore and bluefin. The pH of the inner layer of muscle did not differ appreciably from that of the outer layer. The "ultimate pH" of the muscle did not differ from the pH determined by Partmann's (1960) procedure as recorded in Table I, indicating that lactic acid accumulation in the muscle had reached its maximum value by the time of sampling.

Acid-soluble and acid-labile organic phosphorus compounds (e.g. phosphocreatine and adenosine triphosphate) were at a low concentration in the muscles of all species, while acid-soluble and acid-stable phosphorus compounds were present in moderate amount. Inorganic phosphate accounted for 80–85% of the total acid-soluble phosphorus of the muscle.

These findings for lactic acid and phosphorus fractions are in reasonable agreement with expectations for fish caught under commercial conditions and held at the temperatures and for the periods of time that obtained in this work (Tomlinson *et al.*, 1961, 1963). The lower lactic acid and acid-soluble phosphorus content of the outer $\frac{1}{4}$ inch compared to that of the inner layer indicates some loss of these soluble components (in addition to potassium) may have occurred during freezing (cf. Tomlinson *et al.*, 1962). The relatively high lactic acid content of the muscle of all species was similar to that previously reported for bluefin (Tsuchiya and Kunii, 1960) and for albacore (Tomlinson *et al.*, 1962).

In commercial practice in British Columbia, frozen albacore are thawed in fresh water prior to processing. In Table II data are presented regarding the effects of water thawing on some soluble components of albacore flesh. Data for water-thawed fish subsequently precooked by steaming for 2 hours at 216°F, together with data for air-thawed, precooked fish are also given. The precooking procedure used in this work is somewhat milder than that usually applied to thawed tuna preparatory to canning, but has proved satisfactory under our conditions. The water thawing procedure reduced the sodium content of the outer $\frac{1}{8}$ inch by about 50%, but had little, if any, affect on that of the underlying muscle. The removal of sodium from albacore by water thawing

TABLE I. Sodium, potassium, acid-soluble phosphorus, lactic acid and pH of brine-spray frozen tuna muscle.[a]

Species of tuna and position of sample	Muscle component[b] (mg/g muscle)								
	Na	K	I-P	ML-P	AL-P	AS-P	T-P	Lactic acid	pH
Albacore (1)									
Outer $\frac{1}{8}$"	8.35	2.11							
Next $\frac{1}{4}$"	7.05	1.69	1.36	.073	.027	.235	1.665	7.7	5.72
Inner	0.24	4.23	2.1	.060	.065	.330	2.555	14.9	5.80
Albacore (2)									
Outer $\frac{1}{8}$"	10.60	2.14							
Next $\frac{1}{4}$"	8.37	1.41	1.355	.043	.010	.212	1.620	8.9	5.76
Inner	0.46	4.42	2.095	.083	.092	.272	2.542	16.8	5.60
Bluefin (1)									
Outer $\frac{1}{8}$"	12.4	2.75							
Next $\frac{1}{4}$"	12.2	2.62	1.408	.011	.019	.265	1.703	9.8	5.62
Inner	0.45	4.05	2.095	.027	.038	.361	2.521	16.5	5.68
Bluefin (2)									
Outer $\frac{1}{8}$"	15.8	2.10							
Next $\frac{1}{4}$"	12.4	1.50	1.267	.0	.022	.177	1.460	7.9	5.79
Inner	0.43	4.35	2.105	.001	.026	.428	2.560	13.3	5.62
Skipjack (1)									
Outer $\frac{1}{8}$"	22.1	3.40							
Next $\frac{1}{4}$"	8.17	2.44	1.65	.025	.026	.378	2.079	9.7	5.49
Inner	0.35	4.50	2.14	.018	.041	.381	2.580	15.9	5.43
Skipjack (2)									
Outer $\frac{1}{8}$"	20.2	3.43							
Next $\frac{1}{4}$"	4.97	3.38	1.763	.012	.048	.356	2.179	15.5	5.52
Inner	0.36	4.60	2.139	.033	.051	.337	2.560	16.9	5.44

[a]All fish from a single landing.

[b]Abbreviations: I-P, inorganic phosphorus; ML-P, molybdate labile phosphorus; AL-P, acid-labile phosphorus; AS-P, acid-stable phosphorus: T-P, total acid-soluble phosphorus. (For details of compounds expected in these fractions, see Tomlinson *et al.*, 1962.)

TABLE II. Sodium, potassium, acid-soluble phosphorus, lactic acid and pH of brine-spray frozen albacore muscle, and the influence thereon of thawing and precooking.[a]

Frozen fish	Muscle component (mg/g muscle) Na	K	T-P	Lactic Acid	pH	
(1) Outer ⅛″	10.3	2.79				
Next ¼″	4.08	2.69	2.04	9.6		
Inner	0.24	3.84	2.58	19.2	5.59	
(2) Outer ⅛″	12.4	2.38				
Next ¼″	4.61	2.48	2.01	9.55		
Inner	0.28	3.90	2.51	14.5	5.68	
(3) Outer ⅛″	12.6	2.18				
Next ¼″	5.82	2.54	2.06	9.2		
Inner	0.21	4.41	2.73	14.6	5.58	
Water thawed[b]						
(1) Outer ⅛″	5.7	2.04				
Next ¼″	4.85	2.87	2.22	12.02		
Inner	0.35	4.22	2.76	12.80	5.6	
(2) Outer ⅛″	5.45	2.14				
Next ¼″	5.16	3.03	1.99	8.31		
Inner	0.37	3.51	2.66	13.61	5.52	
(3) Outer ⅛″	5.47	1.39				
Next ¼″	4.12	1.94	1.86	7.78		
Inner	0.28	3.96	2.66	12.92	5.62	
Water thawed and precooked						
(1) Outer ⅛″	5.97	1.91				
Next ¼″	4.02	2.82	2.36	10.24		
Inner	0.20	4.15	2.86	13.63	5.7	
(2) Outer ⅛″	6.80	2.00				
Next ¼″	4.15	2.56	2.28	8.96		
Inner	0.18	3.84	2.72	13.18	5.6	
(3) Outer ⅛″[c]	2.45	1.36				
Next ¼″	1.94	1.79	1.88	8.38		
Inner	0.32	3.84	2.84	11.26	5.7	
Air thawed and precooked[d]					Thawed	Precooked
(1) Outer ⅛″	8.44	1.98				
Next ¼″	2.31	2.62	2.32	9.60		
Inner	0.11	3.77	2.74	14.08	5.64	5.52
(2) Outer ⅛″	11.6	2.14				
Next ¼″	6.91	2.17	1.95	8.83		
Inner	0.14	3.90	2.64	13.69	5.66	5.62
(3) Outer ⅛″	2.45	2.89				
Next ¼″	2.86	2.88	2.03	8.96		
Inner	0.17	4.16	2.94	14.85	5.63	5.59

[a]Fish from a different landing than those in Table I.

[b]Thawed in slowly running water at 10°C for 16 hours.

[c]This sample was from a part of the body from which the skin had been torn prior to our receiving the fish.

[d]Thawed in air at 20°C for 16 hours.

appears to be somewhat less effective than that reported for salt from brine-frozen cod and haddock (Pottinger *et al.*, 1952). The lactic acid and acid-soluble phosphorus content of the muscle beneath the outer $\frac{1}{8}$ inch was also very little affected. Neither thawing (either procedure) nor precooking appears to have had any clearly noticeable influence on the pH of the muscle or on the distribution of the soluble components in it beneath the outer $\frac{1}{8}$ inch.

The data for albacore and bluefin from the third landing examined were similar to those in Tables I and II, with the exception of the values for sodium and potassium in the outer layers of muscle which tended to be somewhat lower and higher, respectively, than those recorded in the Tables. There seems to be some variability between fish in the sodium and potassium content of the outer layer of their muscle, particularly those from different landings.

The relatively high uptake of sodium by the outer layer of muscle in these fish is probably attributable to the high temperature (about 70°F) of the fish at the time of catching and the resulting length of the period of contact between fish and brine before the fish freeze, since precooling of the fish is not practical under the operating conditions of these vessels (S. W. Roach, personal communication; Lang and Farber, 1940). In practice it has been found that the sodium content of the fish after water thawing (a variable proportion of the outer $\frac{1}{4}$ inch of muscle is removed in trimming the fish preparatory to canning) is acceptable for canning, a suitable reduction in the amount of salt added being made to compensate for that already present in the flesh (S. W. Roach, personal communication).

REFERENCES

Callow, E. H. 1938. The "ultimate pH" of muscular tissue. *In* Report of the Food Investigation Board for the year 1937: H. M. Stationery Office, London, p. 49.

Lang, O. W., and L. Farber. 1940. The preservation of tuna by chilled brines. A progress report. Proceedings of the 6th Pacific Science Congress (1939), Vol. III, University of California Press, Berkeley, Calif., pp. 281–289.

Partmann, W. 1960. Rigor- und Gefrierveränderungen bei Süsswasserfischen in Abhängigkeit von der Zeit post mortem. *Arch. Fischereiwiss.*, **11**: 81–105.

Pottinger, S. R., J. Holston and G. McCormack. 1952. Technical note No. 22 — Fish frozen in brine at sea: preliminary laboratory and taste panel tests. *Com. Fish. Rev.*, **14**(7): 20–23.

Roach, S. W., and J. S. M. Harrison. 1963 Tuna freezing equipment for British Columbia seine boats. *Fish. Res. Bd. Canada, Technological Laboratory, Vancouver, Circular* No. 27, 5 pp.

Tomlinson, N., E. S. Arnold, Eve Roberts and S. E. Geiger. 1961. Observations on post mortem biochemical changes in fish muscle in relation to rigor mortis. *J. Fish. Res. Bd. Canada*, **18**: 321–336.

Tomlinson, N., S. E. Geiger and Eve Roberts. 1962. Frozen albacore tuna. The influence of storage conditions prior to freezing. *Fish. Res. Bd. Canada, Prog. Rept. Pacific Coast Sta.*, No. 114, pp. 19–22.

Tomlinson, N., R. E. E. Jonas and S. E. Geiger. 1963 Glycolysis in lingcod muscle during frozen storage. *J. Fish. Res. Bd. Canada*, **20**: 1145–1152.

Tsuchiya, Y., and K. Kunii. 1960. Studies on the influence of the treatments immediately after catching upon the quality of fish flesh. V. Determination of lactic acid in fish muscle. *Bull. Japan. Soc. Sci. Fisheries*, **26**: 284–288.

The Invasion of the Lower Great Lakes by the White Perch, *Roccus americanus* (Gmelin)[1]

By W. B. Scott

Department of Ichthyology and Herpetology
Royal Ontario Museum, University of Toronto, Toronto, Ont.

and W. J. Christie

Research Branch
Ontario Department of Lands and Forests, Glenora, Ont.

ABSTRACT

Roccus americanus (Gmelin) has become part of the Lake Ontario–St. Lawrence River fauna, originating from populations in Upper New York State. The time required for the species to spread through the lower Great Lakes is discussed and summarized. A review of the morphological distinctions of related species is included.

The white perch, *Roccus americanus* (Gmelin), a euryhaline species indigenous to the North American Atlantic coastal plain, has become a significant part of the Lake Ontario fauna since 1950. It would seem worthwhile to document as fully as possible the events leading to this situation in view of the recent spread of the sea lamprey, *Petromyzon marinus* Linnaeus, and the alewife, *Alosa pseudoharengus* (Wilson), from Lake Ontario through Lake Erie to the Upper Great Lakes, particularly since the white perch is now the dominant species in the Bay of Quinte portion of Lake Ontario.

The natural range of the white perch prior to 1950 was the Atlantic coastal plain from Canada's maritime provinces of New Brunswick, Nova Scotia and Prince Edward Island southward to South Carolina. Although generally regarded as a euryhaline species, it readily landlocks and may establish permanent fresh water populations. This is particularly true of New Brunswick and Nova Scotia lakes and we are informed that it is one of the most common species in the Hudson River, below Albany, and in many lakes in the lower Hudson River drainage (Raney, personal communication).

The available evidence suggests that the white perch gained access to Lake Ontario via the Oswego River, as a result of movement by the Hudson River populations northward and westward through the Mohawk River Valley and Erie Barge Canal.

The Biological Survey Report for the Mohawk–Hudson watershed (Anon., 1934) noted that the species was present at lock 7, near Rexford, some 90 miles down the Mohawk River from Oneida Lake (Fig. 1). Eighteen years later Dence (1952) reported that this fish was abundant at Cross Lake. Although published evidence is apparently lacking during these intervening years, the

[1]Received for publication March 7, 1963.

J. Fish. Res. Bd. Canada, **20**(5), 1963.
Printed in Canada.

FIG. 1. Lake Ontario basin, showing the Erie Barge Canal and connecting waters.

white perch was probably gradually extending its range westward along the Mohawk River, through Oneida Lake and along the Seneca River. Whether the species progressed up the Mohawk Valley waterway or whether a short cut was effected by advance introduction by man, will probably never be known. That Dence (1952) was unaware of the origin of the white perch in the Cross Lake region of the Erie Barge Canal system is evident from his statement (p. 200) "Its appearance in Cross Lake is a dark mystery, although one might well assume that it was introduced, as otherwise it would not be so localized."

Dence also remarked that the species was " . . . taken in considerable numbers during the past three or four years at Cross Lake and adjacent parts of the Seneca River as far east as Baldwinsville." Thus the white perch was apparently numerous in Cross Lake and environs as early as 1948 or 1949. To gain access to Cross Lake it is assumed that the fish must traverse Oneida Lake, a large eutrophic lake some 40 river miles to the east and the only large body of water encountered in the Mohawk–Seneca River system (Fig. 1), that is the Erie Barge Canal. To move from Oneida Lake to Cross Lake must have taken at least a year or two — hence we may postulate that the white perch was present in Oneida Lake at least as early as 1946 or 1947.

Attempts to substantiate these dates have, unfortunately, been unsuccessful. Persons familiar with the situation in Oneida Lake have stated that, in their opinion, the white perch invasion occurred about 1950 (Norman Youmans, personal communication) or 1952 (John Forney, personal communication). Information has been sought from many persons concerning the year of first appearance in Oneida Lake but these dates are the only ones obtained. In a more recent paper, Dence (1959) states that entry by white perch to Oneida Lake from the east, via the Oneida River, was greatly facilitated in 1951 by a

change in the type of dam used on this river four miles down river from the lake. This date, 1951, is in agreement with the dates suggested by Youmans and Forney. It is possible that the species went undetected during the period of early build-up and was not reported until it had become well established. A further complicating factor is of course the possibility of unauthorized stocking by anglers. There are specimens in the Cornell research collections taken in the Seneca River in June 1951 and Dr Raney (personal communication) informs us that the collector stated that the species was being taken in the river at least a year earlier (i.e. 1950). Further speculation seems unwarranted for the species was present in the Erie Barge Canal system and capable of passage down the Oswego River, irrespective of whether it came from Oneida Lake on the east, or from populations in the canal system to the west of the Oswego River.

While the white perch populations were building up in the Oneida Lake–Seneca River waters the species was rapidly spreading into Great Lakes waters. Probably sometime between 1946 (the earliest year postulated for Oneida Lake) and 1948 (when Dence estimated they were in the Seneca River), the first white perch moved down the Oswego River and into Lake Ontario.

There are, apparently, no obstacles to free passage down the Oswego River by white perch and there seems no reason to doubt that access to Lake Ontario was gained by this means. As Raney noted (personal communication, 1956), "Up until the time you wrote I had no knowledge of its existence in Lake Ontario, but this should occasion no surprise in view of its abundance in the New York Barge Canal System."

The first positive evidence available to us that this fish was present in the waters of the Great Lakes–St. Lawrence system came from Quebec when Mr. Vianney Legendre, Biological Bureau, University of Montreal, sent two specimens to the Royal Ontario Museum for identification. These were caught in Lake St. Louis, near Montreal in the fall of 1951. In August and October 1952 four more specimens were caught in the St. Lawrence River, this time 260 miles further downstream off Quebec City (Vladykov, 1952).

There is little reason to doubt that the St. Lawrence River captures resulted from the Oswego River entry of *R. americanus*. Vladykov (1952) concluded that downstream migration was the only plausible explanation. There are precedents for downstream movement of a closely related species, since Vladykov (1947) reported the capture of the white bass, *Roccus chrysops* (Rafinesque) off Quebec City. The white bass is widely distributed in Lake Ontario, and this is the closest and most accessible source for the Quebec City records. Vladykov (1945) reported the capture of yet another species off Quebec City, *Dorosoma cepedianum* (LeSueur), and considered its occurrence also to be a result of downstream migration from Lake Ontario.

The possibility that the Quebec records resulted from movement up the St. Lawrence River from the Maritimes cannot be entirely overlooked but the chances are slim indeed. The nearest known populations of white perch on the east are in New Brunswick (Fig. 2). On the east coast of New Brunswick, the Gulf of St. Lawrence side, the white perch is known to occur northward

FIG. 2. St. Lawrence River and Gulf. Northernmost known white perch populations on the east are at Miramichi River, N.B.

to the Miramichi River estuary (Scott and Crossman, 1959). However, there are no records northward of this, and no records for the Baie de Chaleur, nor for the Gaspé Peninsula area nor for the whole of the 400 miles upstream to Quebec City. And there are still no records to indicate that white perch have even moved northward of the Miramichi River (Fig. 2). Thus movement from the east seems highly unlikely and the precedent for movement down the St. Lawrence has already been set by Vladykov's (1945, 1947) reports.

In 1952 at least one specimen was caught in the Bay of Quinte and by 1955 a few specimens per year (less than 50) were being caught in commercial and test netting. From that year onward, however, the species has steadily increased in abundance until by 1957 it was abundant and by 1959 the white perch was the dominant species in the area. In 1960 and 1961 there were signs of stunting but this winter (1962–63), a sudden shift in the size composition has produced marketable quantities of 1–1½ -lb fish. This increase in the average size may be a result of inshore movement by larger fish but other factors, such as predation, may be involved.

In 1953, eleven specimens were seined at the mouth of Highland Creek, 12 miles east of Toronto (ROM cat. no. 17,936). This sample contained two year-classes, including young-of-the-year; hence the species was probably established there at least in 1952.

It should be noted here that Larsen (1954) reported the capture of three specimens in Lake Erie, off Erie, Pennsylvania. The most logical point of entry into this lake would seem to be the Erie Barge Canal which connects with Lake

TABLE I. Appearance of white perch in Great Lakes and contiguous waters, arranged chronologically.

Date	Observation	Authority
1950 (Apr.)	Dence first aware of species in central New York; being caught frequently at this time.	Dence (1952)
1950 (Oct.)	16 fish (3¼ to 3½" total length) young-of-year, seined Cross Lake.	Dence (1952)
1951 (June)	Collection taken in Seneca R., N.Y., ⅛ mile east of Holland Island.	Raney (personal communication)
1951 (Fall)	2 specimens caught in Lake St. Louis, St. Lawrence River, off Montreal. (sent to Royal Ontario Museum for identification).	Vladykov (1952)
1952 (Aug.–Oct.)	4 specimens caught in St. Lawrence River in vicinity of Quebec City.	
1952	1 specimen at least caught in Bay of Quinte, Lake Ontario.	W. J. Christie (G.F.S. collection)
1953 (July)	11 specimens (117–201 mm total length), young-of-year and adults seined 12 miles east of Toronto, Lake Ontario.	R.O.M. collection[b]
1953	3 specimens reported off Erie, Pa.	Larsen (1954)
1952–1957	Population build-up taking place in Bay of Quinte.	W. J. Christie
1957	Abundant in Bay of Quinte.	
1959	Dominant species in Bay of Quinte.	
1959	1 specimen (230 mm total length) taken mouth of Niagara River, Ontario.	D. Roseborough R.O.M. collection
1960	1 specimen (215 mm total length) caught off Port Credit, Lake Ontario.	R.O.M. collection
1961 (Dec.)	1 specimen, Welland Canal, lock 7, near Thorold, 8 miles upstream from Lake Ontario; by electric shocker.	D. P. Dodge R.O.M. collection

[a]Glenora Fisheries Station, Ontario Department of Lands and Forest, Glenora, Ont.
[b]Royal Ontario Museum, University of Toronto, Toronto 5, Ont.

Erie at Buffalo. Trautman (1957) reviewed the occurrence in Lake Erie, but was unable to verify the presence of the white perch in Ohio waters.[2] Although biologists on both sides of Lake Erie have been on the watch no more specimens have been reported.

By 1960 the white perch had been recorded in many localities along the Ontario shoreline of Lake Ontario, including the mouth of the Niagara River. There is little or no information that would indicate the abundance of the species west of the Bay of Quinte. There is practically no commercial fishing activity west of the Quinte region in Lake Ontario and reports of any kind are difficult to obtain.

In 1961 a small specimen was taken by a Fisheries Research Board of Canada survey team at lock 7 near Thorold, Ontario, in the Welland Canal about 8

[2]The Larsen (1953) and Trautman (1957) accounts of the dates of capture in Lake Erie in 1953 do not agree. Larsen's dates are June 20, July 20, July 27, while Trautman gives June 20 and June 27.

TABLE II. Comparison of morphological differences in the species of *Roccus* occurring in the St. Lawrence River drainage.

Character	*Roccus*[a]		
	americanus	*saxatilis*	*chrysops*
Dorsal fins:	slightly joined by membrane	entirely separate	entirely separate
Soft anal rays:	9 or 10	10 or 11	12 or 13
Anal spines: (III)	not graduated; 2nd and 3rd spines subequal; spines stout; longest spines $\frac{3}{4}$ or more the height of fin	graduated in length; more slender than *americanus* or *chrysops*: longest spine less than $\frac{1}{2}$ the height of fin	graduated in length; more slender than *americanus*: longest spine equal to or greater than $\frac{1}{2}$ the height of the fin
Base of tongue:	without teeth	with teeth	with teeth
Body colour:	silvery, somewhat brassy in Lake Ontario[b], without conspicuous lateral stripes; chin pink to purple, blue when spawning	silvery with about 7 conspicuous lateral stripes; chin white	silvery with 4 or 5 conspicuous lateral stripes; chin white

[a]For more detail on osteological features, see Woolcott (1957).

[b]Contrary to most colour descriptions, the white perch in Lake Ontario frequently exhibited brassy reflections, and some commercial fishermen reported that it resembled a yellow perch, but without bars.

miles upstream from Lake Ontario. A summary of the data concerning first reports and relative abundance is presented in Table I.

That the white perch will eventually become established in Lake Erie seems inevitable. The puzzle is why there has been only the one Pennsylvania report — why haven't more white perch escaped into Lake Erie from the Erie Barge Canal system? Whatever the reason, the Welland Canal, which has been used so successfully by the sea lamprey and other fishes is again being used by a migrant species.

To facilitate identification of white perch a comparison of the serranid fishes known to occur in the St. Lawrence River system is presented in Table II.

ACKNOWLEDGMENTS

We are grateful to the many fishermen and biologists who have supplied us with specimens and information. We are especially grateful to Dr J. R. Greeley, New York Conservation Department, and Dr E. C. Raney of Cornell University, for information regarding the white perch in New York State, and to Mr D. P. Dodge, Fisheries Research Board of Canada, Messrs D. Roseborough and Roy Muma, Ontario Department of Lands and Forests, and Mr Nelson Anderson, Port Credit, Ontario, who have generously supplied specimens and information.

REFERENCES

ANON. 1934. A biological survey of the Mohawk-Hudson watershed. *New York Conservation Dept. Biol. Survey*, No. 9, pp. 1–379.

DENCE, W. A. 1952. Establishment of white perch, *Morone americana*, in central New York. *Copeia* for 1952, No. 3, pp. 200–201.

DENCE, W. A., AND D. F. JACKSON. 1959. Changing chemical and biological conditions in Oneida Lake, New York. School of Science and Mathematics, April, pp. 317–324.

LARSEN, A. 1954. First record of the white perch (*Morone americana*) in Lake Erie. *Copeia* for 1954, No. 2, p. 154.

SCOTT, W. B., AND E. J. CROSSMAN. 1959. The freshwater fishes of New Brunswick: a checklist with distributional notes. *Contrib. Royal Ontario Museum, Div. Zool. and Palaeont.*, No. 51, pp. 1–37.

TRAUTMAN, M. B. 1957. The fishes of Ohio. Ohio State Univ. Press, pp. 1–683.

VLADYKOV, V. D. 1945. Trois poissons nouveaux pour la Province de Québec. *Naturaliste Canadien*, Québec, **73**(1, 2): 27–39.

1947. Nouveau bar (*Lepibema chrysops*) pour la Province de Québec. *Ibid.*, **74**(7, 8): 195–206.

1952. Présence dans le Québec du *Morone americana*, troisième espèce des serranidés. *Ibid.*, **79**(12): 325–329.

WOOLCOTT, W. S. 1957. Comparative osteology of serranid fishes of the genus *Roccus* (Mitchill). *Copeia* for 1957, No. 1, pp. 1–10.

Tidal Calibration of the Hecate Model[1]

By W. H. Bell and N. Boston

Fisheries Research Board of Canada
Pacific Oceanographic Group, Nanaimo, B.C.

ABSTRACT

A semi-empirical method for the tidal calibration of oceanographic models with two ocean approaches is developed. The same method may be extended to models with more than two approaches. Tidal functions (amplitude and phase) at reference stations are expressed in terms of the amplitudes and phases of the tide generators. A Taylor expansion is made about an initial set of conditions imposed on the generators. The result is a set of simultaneous equations, whose coefficients can be found experimentally. Then, knowing the response at the reference points to the initial generator conditions, corrections can be made to obtain any desired tide.

The method is applied to the particular case of the Hecate Model. Examples of single- and multiple-component tides are given.

INTRODUCTION

The Hecate model (Fig. 1) has been described by Bell and Boston (1962). It is an oceanographic model of the region including Dixon Entrance, Queen Charlotte Sound and Hecate Strait (Fig. 2). This region is about 350 nautical miles long and averages 80 miles in width. The model scales are:

Vertical	—	1:300
Horizontal	—	1:24,320
Time	—	1:1404
Velocity	—	1:17.3

Figure 1 shows the model complex and the relationship between the various components. Tides are generated by two computer-controlled tilting plates. The resultant vertical displacement of the water surface is measured by electronic tide gauges and recorded on an 8-channel recorder. The camera is located 90 feet above the surface. It is used to photograph floats or dye patches in connection with current studies.

Before the model can be made to yield useful information, it is necessary to generate in it a reasonable representation of the prototype tide. This is accomplished by feeding appropriate data into the tide computers. A method for obtaining these data in a model having any number of tide generators is developed below and applied specifically to the Hecate Model.

Simulation of Prototype Tides

The theory of tides has been adequately discussed by Marmer (1926), Doodson and Warburg (1941), Schureman (1941), and others. It is shown that

[1]Received for publication January 28, 1963.

J. Fish. Res. Bd. Canada, 20(5), 1963.
Printed in Canada.

the height of the tide T at a time t, in any locality, can be expressed by the sum of a series of harmonic terms of the form

$$T = H_0 + \sum_i A_i \cos(\omega_i t + \phi_i) \quad (1)$$

where H_0 is the height of mean sea level, A_i is the amplitude of the i^{th} harmonic term, or component, ω_i is the angular velocity of the i^{th} component, and ϕ_i is the phase of the i^{th} component at time $t = 0$ (defined as January 1, 0000 hrs for any given year). At any position in the sea, the quantities A_i and ϕ_i are the harmonic constants. They are determined from a continuous record of the tide covering a considerable period of time and are, therefore, known at coastal positions only. The preliminary problem of tidal models is to find the motion of the tide generators which will reproduce the correct harmonic constants at the corresponding coastal positions.

In the case of a simple basin, with a single approach from the ocean, the generator is adjusted to produce the known tide at a single reference station. To achieve similarity at other stations, it is necessary to adjust the roughness of the model basin to provide the required local accelerations. The reliability

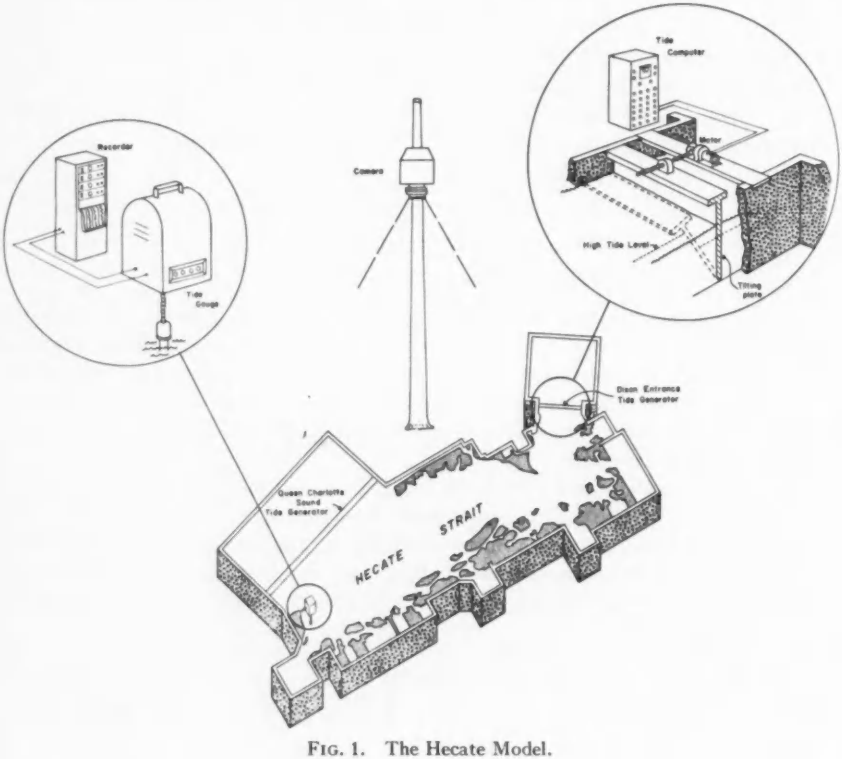


FIG. 1. The Hecate Model.

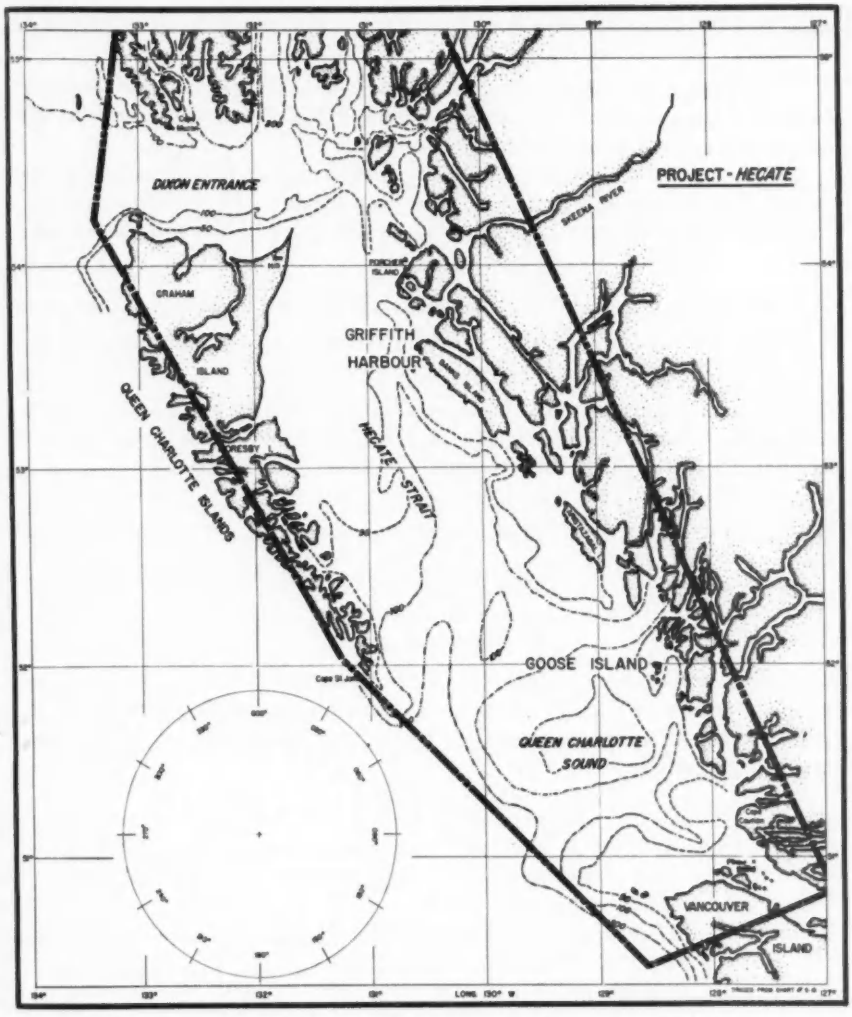


FIG. 2. The Hecate region. Scale is 60 nautical miles per degree of latitude.

of the model increases with the number of similarities established. In other cases, using the method developed below, the behaviour of the generators is uniquely defined when similarity between model and prototype is established at the same number of reference stations as there are ocean approaches (i.e. tide generators). The requirement for an equal number of generators and reference points arises from the necessity of having a square matrix for the mathematical computations[2].

[2]The computations involve the inverse of a matrix. Only non-singular matrices have inverses and all non-singular matrices are square.

Analysis of Model Response to Tide Generator Motion

Single-component tide

The method of analysis is described for the special case of two tide generators (since the Hecate Model has two generators). The generalization of the procedure to n generators will be obvious.

Assume that, in an oceanographic model having two tide generators g_1 and g_2, two reference points p_1 and p_2 have been chosen. For a single harmonic component, the motion of g_1 (defined by an amplitude a_1 and a frequency ω) is

$$G_1 = a_1 \cos \omega t \tag{2}$$

The motion of g_2 is similar, with the addition of an angle θ to designate the phase difference between the generators. Therefore

$$G_2 = a_2 \cos (\omega t + \theta) \tag{3}$$

The resultant responses of the water surface at p_1 and p_2 are characterized by amplitudes b_1 and b_2, respectively. Phase difference between the points is designated by an angle ϕ. The responses are, then,

$$\begin{aligned} P_1 &= b_1 \cos \omega t \\ P_2 &= b_2 \cos (\omega t + \phi) \end{aligned} \tag{4}$$

where

$$\begin{aligned} b_1 &= b_1 (a_1, a_2, \theta) \\ b_2 &= b_2 (a_1, a_2, \theta) \\ \phi &= \phi (a_1, a_2, \theta) \end{aligned} \tag{5}$$

Consider the response (b_1^0, b_2^0, ϕ^0) of the model, resulting from a given generator setting (a_1^0, a_2^0, θ^0), as a first approximation to the correct tide (b_1, b_2, ϕ). A Taylor series expansion can be made about this initial, or reference, state. The result is

$$\begin{aligned} b_1 &= b_1^0 + \frac{\delta b_1}{\delta a_1}\bigg|_0 da_1 + \frac{\delta b_1}{\delta a_2}\bigg|_0 da_2 + \frac{\delta b_1}{\delta \theta}\bigg|_0 d\theta \\ b_2 &= b_2^0 + \frac{\delta b_2}{\delta a_1}\bigg|_0 da_1 + \frac{\delta b_2}{\delta a_2}\bigg|_0 da_2 + \frac{\delta b_2}{\delta \theta}\bigg|_0 d\theta \\ \phi &= \phi^0 + \frac{\delta \phi}{\delta a_1}\bigg|_0 da_1 + \frac{\delta \phi}{\delta a_2}\bigg|_0 da_2 + \frac{\delta \phi}{\delta \theta}\bigg|_0 d\theta \end{aligned} \tag{6}$$

neglecting higher order terms. In this expression, the unknowns are the nine partial derivative coefficients ($\frac{\delta b_i}{\delta a_j}$, $\frac{\delta b_i}{\delta \theta}$, $\frac{\delta \phi}{\delta a_j}$ and $\frac{\delta \phi}{\delta \theta}$ where $i, j = 1, 2$) and the differentials da_j and $d\theta$. The partial derivatives express changes in reference point amplitudes and phase with respect to unit changes in generator amplitudes and phase. They can be determined experimentally at the initial state. The differentials correspond to corrections which must be applied to the initial generator settings to obtain the correct tide at the reference points. The result of neglecting terms above the first order is a system of linear equations. This is much easier to use in practice than a system of non-linear equations. Although the linear set is valid only in a small range about the initial setting, the method

is justified since the intended procedure is to guess initial generator settings which give a response reasonably close to the desired one. Thus, equations 6 are a set of three simultaneous equations in three unknowns, with constant coefficients. Expressed in matrix form, they become

$$\begin{bmatrix} b_1 - b_1^0 \\ b_2 - b_2^0 \\ \phi - \phi^0 \end{bmatrix} = \begin{bmatrix} \frac{\delta b_1}{\delta a_1} & \frac{\delta b_1}{\delta a_2} & \frac{\delta b_1}{\delta \theta} \\ \frac{\delta b_2}{\delta a_1} & \frac{\delta b_2}{\delta a_2} & \frac{\delta b_2}{\delta \theta} \\ \frac{\delta \phi}{\delta a_1} & \frac{\delta \phi}{\delta a_2} & \frac{\delta \phi}{\delta \theta} \end{bmatrix} \begin{bmatrix} da_1 \\ da_2 \\ d\theta \end{bmatrix} \tag{7}$$

Solving for the differentials gives

$$\begin{bmatrix} da_1 \\ da_2 \\ d\theta \end{bmatrix} = \begin{bmatrix} \frac{\delta b_1}{\delta a_1} & \frac{\delta b_1}{\delta a_2} & \frac{\delta b_1}{\delta \theta} \\ \frac{\delta b_2}{\delta a_1} & \frac{\delta b_2}{\delta a_2} & \frac{\delta b_2}{\delta \theta} \\ \frac{\delta \phi}{\delta a_1} & \frac{\delta \phi}{\delta a_2} & \frac{\delta \phi}{\delta \theta} \end{bmatrix}^{-1} \begin{bmatrix} b_1 - b_1^0 \\ b_2 - b_2^0 \\ \phi - \phi^0 \end{bmatrix} \tag{8}$$

The new settings of the tide generators are then

$$\begin{aligned} a_1 &= a_1^0 + da_1 \\ a_2 &= a_2^0 + da_2 \\ \theta &= \theta^0 + d\theta \end{aligned} \tag{9}$$

MULTIPLE-COMPONENT TIDE

Generator movement for a multiple-component tide can be described by

$$G_i = \Sigma\, a_{ij} \cos\,(\omega_j t + \theta_{ij}) \tag{10}$$

where a_{ij} is the amplitude of the j^{th} component on the i^{th} generator, ω_j is the frequency of the j^{th} component, and θ_{ij} is the phase of the j^{th} component on the i^{th} generator relative to some arbitrary reference time. The Hecate Model computers can represent the effect of seven components (Table I) so that, in this case, $i = 1, 2$ and j has values from 1 through 7.

Reference point response is given by

$$P_i = \Sigma\, b_{ij} \cos\,(\omega_j t + \phi_{ij}) \tag{11}$$

where b_{ij} is the amplitude of the j^{th} component at the i^{th} reference point, and ϕ_{ij} is the phase of the j^{th} component at the i^{th} reference point relative to some arbitrary time.

The principal tide producing forces have either diurnal or semi-diurnal periods. Within either of these two groups, the ratios of periods differ only slightly from unity. However, the ratio of average periods of the groups themselves is approximately two. Therefore, assuming the model is not sensitive to small frequency differences, it is only necessary to consider two frequency groups, rather than individual frequencies.

TABLE I. Harmonic components used in the Hecate Model.

Symbol	Name of component	Period (hours)
M_2	Principal lunar semidiurnal	12.421
S_2	Principal solar semidiurnal	12.000
N_2	Larger lunar elliptic semidiurnal	12.658
K_2	Luni-solar declinational semidiurnal	11.967
K_1	Luni-solar declinational diurnal	23.934
O_1	Principal lunar declinational diurnal	25.819
P_1	Principal solar declinational diurnal	24.066

The amplitudes and phases for each frequency group can be expressed as slowly varying functions of time. This allows equations 10 and 11 to be written

$$G_i = a_i(t) \cos [\omega t + \theta_i(t)] \tag{12}$$

$$P_i = b_i(t) \cos [\omega t + \phi_i(t)] \tag{13}$$

In these expressions, ω can be thought of as the weighted mean frequency of the group being considered. The periods of $a_i(t)$ and similar variables will be at least of the order of 15 to 30 times greater than the periods of the diurnal and semi-diurnal components.

The frequency components enter the variables in a non-linear fashion, introducing harmonics. To simplify analysis, these harmonics are neglected. Thus, it is assumed that the system is linear and no frequency coupling takes

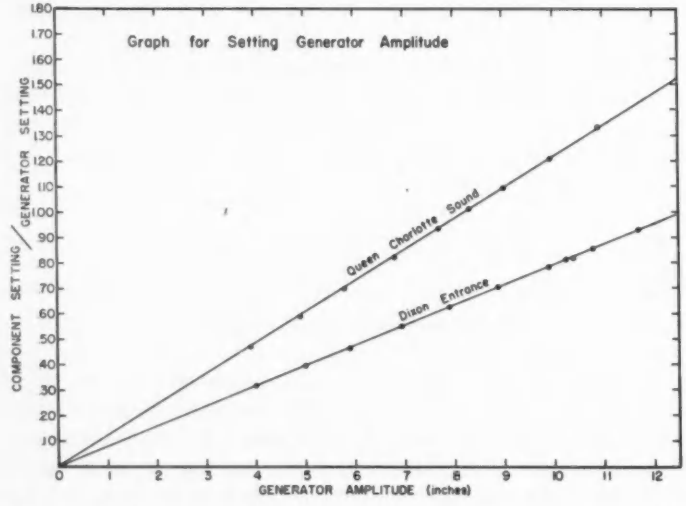


FIG. 3. Graph of component setting/generator setting vs generator amplitude.

place. (Experiment indicates that non-linear effects in the Hecate Model are small.) Then it can be expected that the following equations will be satisfied:

$$b_i(t) - b_i^0 = \frac{\delta b_i}{\delta a_j} da_j + \frac{\delta b_i}{\delta \theta_j} d\theta_j$$

$$\phi_i(t) - \phi_i^0 = \frac{\delta \phi_i}{\delta a_j} da_j + \frac{\delta \phi_i}{\delta \theta_j} d\theta_j \tag{14}$$

Therefore, the problem is essentially reduced to the addition of single-component cases.

Experimental Procedure

Computer calibration

In "setting up" the Hecate Model tide computers, voltages representing component amplitudes are applied across corresponding sine-cosine potenti-

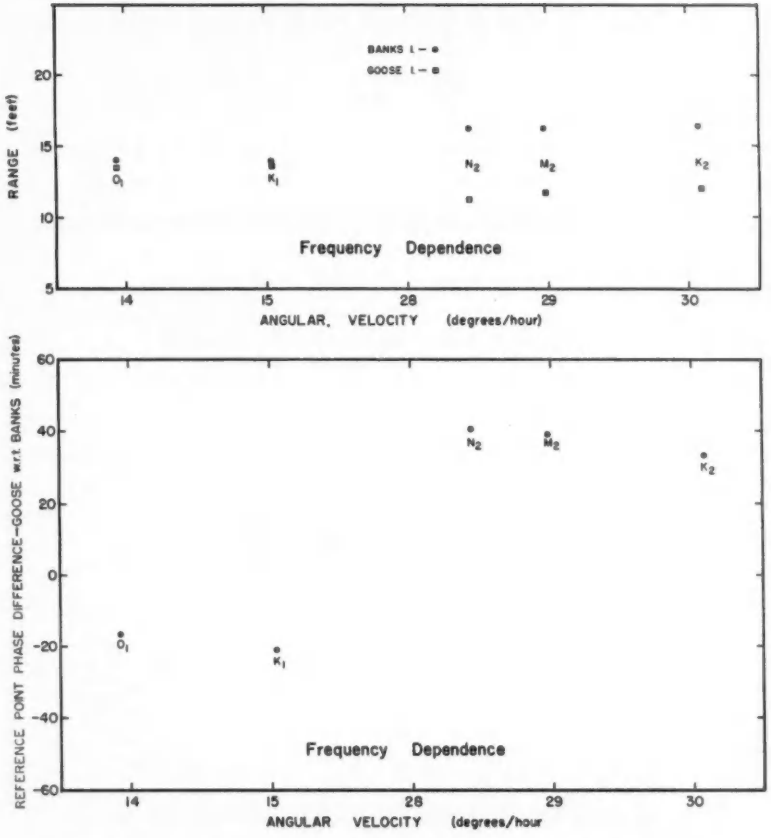


FIG. 4. Frequency dependence of reference point range and phase difference.

ometers. The potentiometers are then rotated at the correct component speeds and their outputs summed. Also forming part of the sum is a voltage, known as the generator voltage, by which the maximum generator amplitude can be fixed. Therefore, the first requisite for obtaining tides in the model is a relationship between the foregoing voltages and the resultant generator amplitude. This relationship is shown graphically in Fig. 3.

TIDAL CALIBRATION

In the Hecate Model, one tide generator is across Dixon Entrance (DE) and the other is across Queen Charlotte Sound (QCS). Reference points were chosen at Goose Island (G) and Banks Island (B), the harmonic constants being known at these locations. Equation 8 may, therefore, be written

$$\begin{bmatrix} da_{DE} \\ da_{QCS} \\ d\theta \end{bmatrix} = \begin{bmatrix} \frac{\delta b_B}{\delta a_{DE}} & \frac{\delta b_B}{\delta a_{QCS}} & \frac{\delta b_B}{\delta \theta} \\ \frac{\delta b_G}{\delta a_{DE}} & \frac{\delta b_G}{\delta a_{QCS}} & \frac{\delta b_G}{\delta \theta} \\ \frac{\delta \phi}{\delta a_{DE}} & \frac{\delta \phi}{\delta a_{QCS}} & \frac{\delta \phi}{\delta \theta} \end{bmatrix}^{-1} \begin{bmatrix} b_B - b_B^0 \\ b_G - b_G^0 \\ \phi - \phi^0 \end{bmatrix} \quad (15)$$

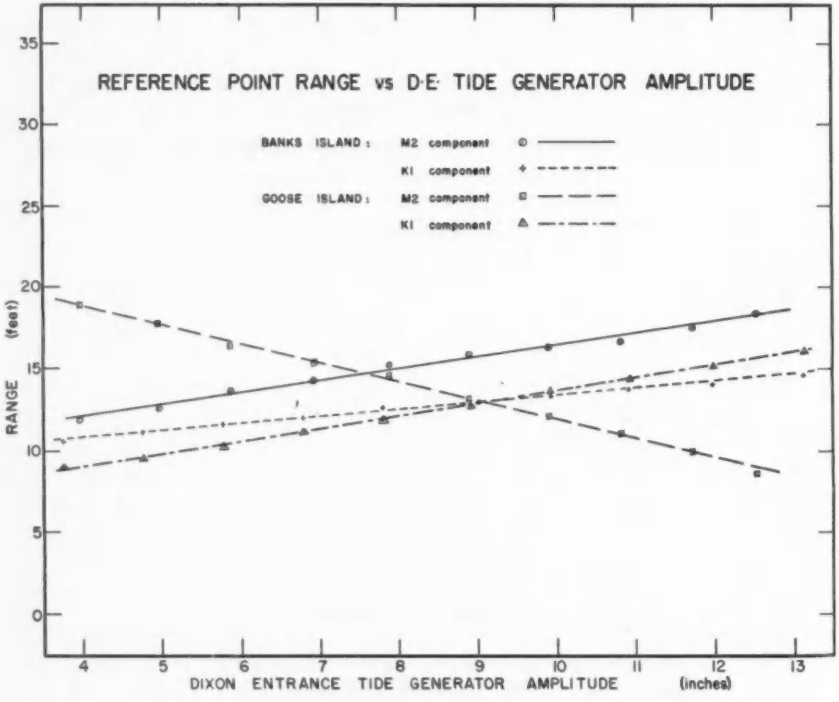


FIG. 5. Reference point range vs D.E. tide generator amplitude.

Inversion of the matrix does not destroy the dimensional homogeneity of each equation of the set.

A reference state was chosen (on the basis of some preliminary trials) with generator amplitude and phase settings of

$$\begin{aligned} a^0_{DE} &= 10.3 \text{ inches} \\ a^0_{QCS} &= 5.8 \text{ inches} \\ \theta^0 &= 9.5 \text{ degrees} \end{aligned} \tag{16}$$

where positive values of θ indicate the Queen Charlotte Sound generator is leading the Dixon Entrance generator. Individual trials were made, using these reference state values, with each of five different harmonic components. The results of these trials are shown in Fig. 4. It is evident from the figure that the variation of both amplitude and phase, with small changes in frequency, is slight. Therefore, basing the calibration on one diurnal component (K_1) and one semi-diurnal component (M_2) is justified. (These two components have the largest amplitudes in their respective frequency groups.)

A multitude of tide trials were made for the calibration proper. One tide generator term was varied, with the remaining two terms being held at the reference state values, and the response terms were measured. The resulting

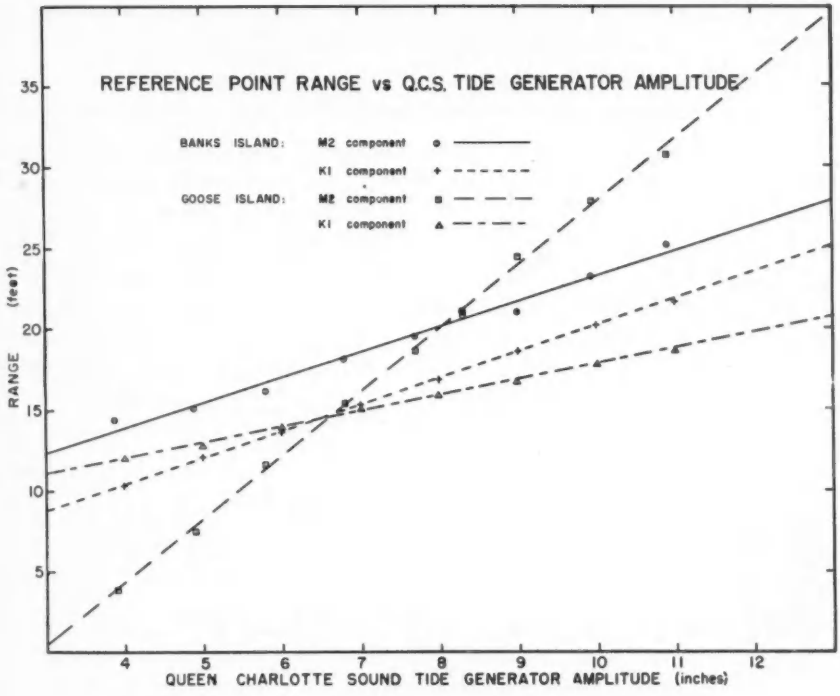


FIG. 6. Reference point range vs QCS tide generator amplitude.

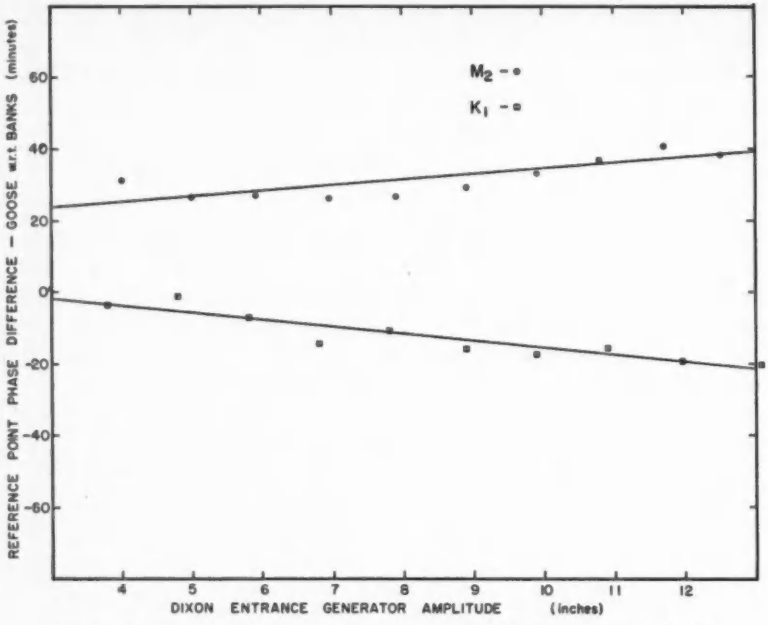


FIG. 7. Reference point phase difference vs DE tide generator amplitude.

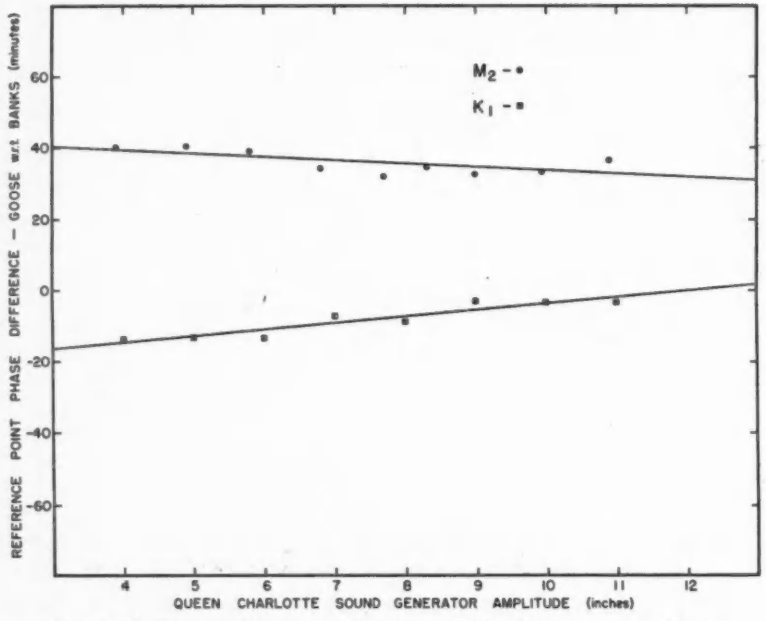


FIG. 8. Reference point phase difference vs QCS tide generator amplitude.

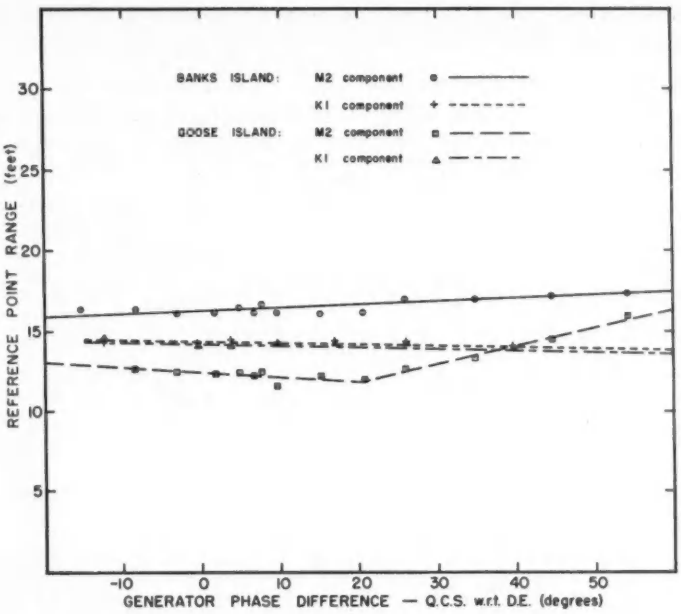


FIG. 9 Reference point range vs tide generator phase difference.

relationships between generator and response terms appeared to be very nearly linear, within reasonable limits of variation. Therefore, straight lines were fitted by the method of least mean squares. These curves are shown, for both the M_2 and K_1 components, in Fig. 5 through 10.

The coefficients in the Taylor series expansion were obtained from the slopes of the curves (Table II). (Note that the coefficients involve amplitudes, whereas the curves are plotted in terms of range.) The inverse matrices to be used in the Hecate Model equations are then

$$\left[\begin{array}{lll} 0.37 & 0.78 & 0.01 \\ -0.59 & 1.95 & -0.02\ (\theta < 20^\circ) \\ & & 0.06\ (\theta > 20^\circ) \\ 1.47 & -0.98 & 3.31\ (\theta < 20^\circ) \\ & & 2.27\ (\theta > 20^\circ) \end{array}\right] \text{semidiurnal} \qquad (17)$$

and

$$\left[\begin{array}{lll} 0.21 & 0.82 & -0.01 \\ 0.39 & 0.48 & -0.01 \\ -1.97 & 1.82 & -1.48 \end{array}\right] \text{diurnal} \qquad (18)$$

Normally, θ is less than 20°. It is always measured in degrees. ϕ must be in terms of prototype minutes.

Reproduction of Tides in the Model

The calibration matrices having been obtained, it is possible to reproduce any desired tide in the model. The calculations leading to the establishment of a single-component (M_2) tide are shown in Table III.

A more particular requirement may be the duplication of a prototype tide during a certain specific period. In such a case, it is necessary to program the computer for a tide commencing about a month before the desired period. This allows initial transient fluid motions in the model basin to subside.

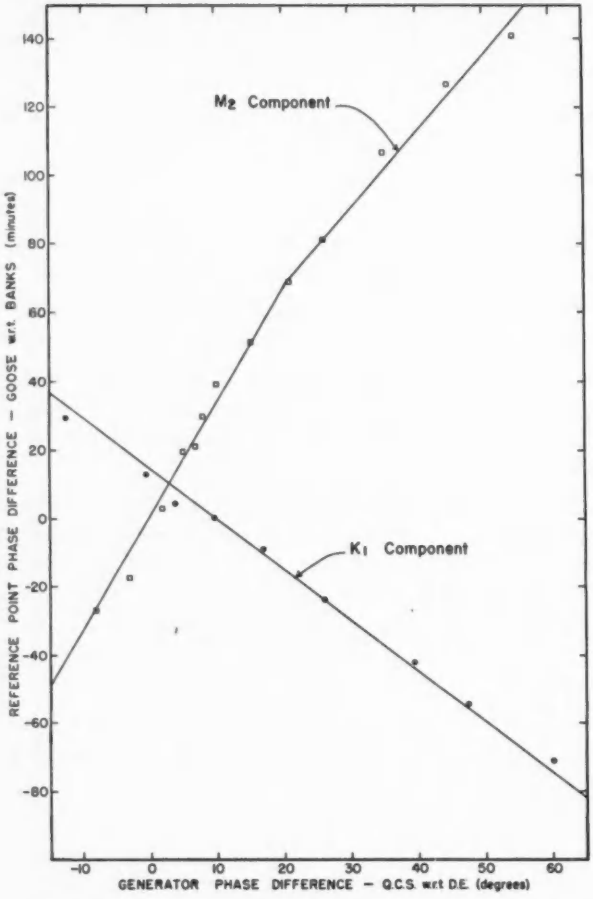


FIG. 10. Reference point phase difference vs generator phase difference.

TABLE II. Calibration curve formulae. (Abbreviations: gen. amp. = generator amplitude; ref. pt. = reference point; diff. = difference; QCS = Queen Charlotte Sound; DE = Dixon Entrance; θ = generator phase difference.)

Ordinate	Abscissa	Component	Equation
QCS gen. amp. (inches)	Banks Is. range (feet)	M_2	$y = 1.56x + 7.66$
" " " "	" " "	K_1	$y = 1.63x + 3.93$
" " " "	Goose Is. Range (feet)	M_2	$y = 3.90x - 11.21$
" " " "	" " "	K_1	$y = 0.96x + 8.21$
" " " "	Ref. pt. phase diff. (min)	M_2	$y = -0.98x + 43.47$
" " " "	" " "	K_1	$y = 1.82x - 21.83$
DE " " "	Banks Is. range (feet)	M_2	$y = 0.73x + 9.16$
" " " "	" " "	K_1	$y = 0.42x + 9.24$
" " " "	Goose Is. range (feet)	M_2	$y = -1.17x + 23.57$
" " " "	" " "	K_1	$y = 0.78x + 5.92$
" " " "	Ref. pt. phase diff. (min)	M_2	$y = 1.47x + 19.47$
" " " "	" " "	K_1	$y = -1.97x + 3.95$
θ (degrees)	Banks Is. range (feet)	M_2	$y = 0.02x + 16.24$
" "	" " "	K_1	$y = -0.01x + 14.37$
" " ($\theta < 20°$)	Goose Is. range (feet)	M_2	$y = -0.03x + 12.45$
" " ($\theta > 20°$)	" " "	M_2	$y = 0.11x + 9.67$
" "	" " "	K_1	$y = -0.01x + 14.35$
" " ($\theta < 20°$)	Ref. pt. phase diff. (min)	M_2	$y = 3.31x + 1.52$
" " ($\theta > 20°$)	" " "	M_2	$y = 2.27x + 22.32$
" "	" " "	K_1	$y = -1.48x + 14.51$

Consideration must be given to the generator settings for the first approximation tide. Experience with the Hecate Model has shown a good starting point to be the tidal equations (Shureman, 1941) of the primary reference points. The equation at each reference point is used to control the tide generator nearest that point. Maximum generator amplitudes are chosen (again previous experience is useful) and the computer voltages found from Fig. 3.

Tide response values are obtained from the recorder output and compared to the desired quantities. The differences are averaged in groups over a suitable period of time. The groups are chosen to contain values at alternate high waters and alternate low waters. Then, for example, if the averages of both high-water groups differ from zero by the same amount, the semi-diurnal component values are in error. If one average is zero and the other is not zero, the diurnal component values are wrong. If both averages differ from zero by different amounts, then both diurnal and semi-diurnal component values must be changed. Using this procedure, it is not possible to assign errors to individual components but only to the two frequency sets. The corrections, as obtained from the matrix equations, are then distributed proportionally to components within a set and a second-approximation tide is generated. This should approach the desired tide within the expected limits of error.

Errors associated with a first-approximation tide for the month of July 1960 are shown in Fig. 11. Only five components were used. The model response was compared with 5-component tide tables prepared on a digital

computer (Bell, 1962), although published tide tables (Anon., 1960) would have been satisfactory. It is not feasible to use prototype tide records for the comparison because atmospheric effects may cause significant differences between predicted and actual tides.

TABLE III. Establishment of a single-component (M_2) tide (all model tidal values have been scaled to equivalent prototype values).

1. Desired tide
   - Amplitude at Banks Is. $b_B = 6.0$ ft
   - Amplitude at Goose Is. $b_G = 4.1$ ft
   - Phase difference (Goose leading Banks) $\phi = 29$ min
2. Initial generator settings
   - Amplitude of DE generator $a_{DE} = 6.6$ in
   - Amplitude of QCS generator $a_{QCS} = 3.6$ in
   - Phase difference (QCS leading DE) $\theta = 15$ deg
3. Initial resultant tide
   - Amplitude at Banks Is. $b_B^0 = 5.4$ ft
   - Amplitude at Goose Is. $b_G^0 = 3.8$ ft
   - Phase difference (Goose leading Banks) $\phi^0 = 68$ min
4. Deviation of resultant from desired tide
   - $b_B - b_B^0 = 6.0 - 5.4 = 0.6$ ft
   - $b_G - b_G^0 = 4.1 - 3.8 = 0.3$ ft
   - $\phi - \phi^0 = 29 - 68 = -39$ min
5. Computed tide generator corrections (from equations 15 and 17)
   - $da_{DE} = 1.2$ in
   - $da_{QCS} = 0.4$ in
   - $d\theta = -12$ deg
6. New generator settings
   - $a_{DE}^1 = 6.6 + 1.2 = 7.8$ in
   - $a_{QCS}^1 = 3.6 + 0.4 = 4.0$ in
   - $\theta^1 = 15 - 12 = 3$ deg (QCS leading DE)
7. New resultant tide
   - $b_B^1 = 6.4$ ft
   - $b_G^1 = 3.8$ ft
   - $\phi^1 = 26$ min

These values are within the expected limits of error, so this resultant is accepted as the desired tide.

Sources of Error

Each step of a tidal experiment, from the introduction of a tide into the model to the extraction of the desired data, involves cumulative errors. The estimation of individual error magnitudes and their summation to provide a maximum error value is not satisfactory. Therefore, a number of single-com-

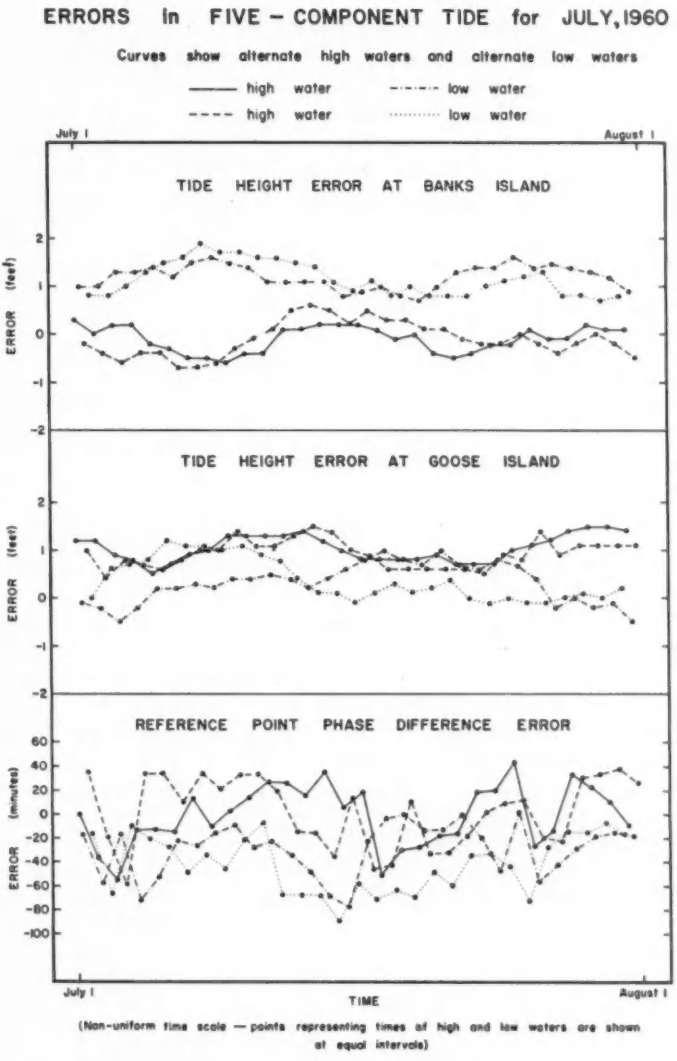


Fig. 11. Errors in first approximation tides at Banks and Goose Islands.

ponent semi-diurnal tide trials were made in each of which the in put values were the same. Output values (i.e. tide heights and phases) were examined to give estimated maximum errors. These proved to be ±15 prototype minutes in reference point phase difference and ±1.5 prototype feet in tidal range. Standard deviations (S) were

$$\begin{aligned} S_{range} \text{ at Banks Island} &= 0.3 \text{ feet} \\ S_{range} \text{ at Goose Island} &= 0.6 \text{ feet} \\ S_{phase\ difference} &= 4.4 \text{ minutes} \end{aligned} \tag{19}$$

with mean values of

$$\begin{aligned} \bar{b}_B &= 12.6 \text{ feet} \\ \bar{b}_G &= 7.1 \text{ feet} \\ \bar{\phi} &= 25.9 \text{ minutes} \end{aligned} \tag{20}$$

These apply to single-component tides only. Multiple-component tide errors have not yet been examined in detail but it is anticipated that the squares of the standard deviations for each component will be additive, i.e.

$$S^2_{tide\ range} = S^2_{M_2\ range} + S^2_{K_1\ range} + \ldots .$$

ACKNOWLEDGMENTS

We are grateful to Dr J. P. Tully who initiated and directed this research, and to Dr N. P. Fofonoff who made invaluable suggestions and carried out the multiple-component analysis in detail.

REFERENCES

ANON. 1960. Pacific Coast Tide and Current Tables. Dept. of Mines and Technical Surveys, Ottawa, 257 pp.

BELL, W. H. MS, 1962. Tide predicting with TIDAC. *Fish. Res. Bd. Canada, Oceanogr. and Limnol. MS Rept. Series*, No. 130.

BELL, W. H., AND N. BOSTON. MS, 1962. The Hecate Model. *Fish. Res. Bd. Canada, Oceanogr. and Limnol. MS Rept. Series* No. 110.

DOODSON, A. T., AND H. D. WARBURG. 1941. Admiralty Manual of Tides. Hydrographic Department, Admiralty, London, 270 pp.

MARMER, H. A. 1926. The tide. D. Appleton and Co., New York, 282 pp.

SCHUREMAN, P. 1941. Manual of harmonic analysis and prediction of tides. U.S. Govt. Printing Office, Washington, 317 pp.

Vital Statistics of *Esox masquinongy* in Nogies Creek, Ontario. I. Tag Loss, Mortality Due to Tagging, and the Estimate of Exploitation[1,2]

By Barry S. Muir[3]

University of Toronto, Toronto 5, Ontario

ABSTRACT

A small population of maskinonge was exploited by a 9-year fishery, using fixed nets under control of the investigator. During the period 1952 to 1960, approximately 4000 maskinonge were handled, 2000 of them being tagged and returned to the population.

The rate of loss of the preopercular disc tag increased progressively with time out, so that an estimated 8.5% of the tags had been lost after the end of the first year, 30% after the second and virtually all after the third. The total mortality and tag loss is estimated to range from 25% to 66% during the period from spring to fall for various years. These estimates are used as correcting factors to determine the numbers of tags extant at the start of the fall fishery each year. The rates of recapture of these tags give estimates of exploitation during the fall fisheries, and the average coefficient of catchability, derived from these data, is 0.0026 for fish age IV and older.

A method, using simultaneous tag and recapture data, is developed to estimate the coefficient of catchability for each age-group. The estimated coefficients of catchability increase, almost linearly, from 0.0013 for age-group III to 0.0032 for age-group VI+. The average coefficient estimated by this method, 0.0025 for age-group IV and older, agrees well with that estimated independently by the method above.

INTRODUCTION

As has been frequently pointed out, reliable estimates of the size of the population, its age composition, and its rates of mortality are essential for any consideration of the productivity of a fishery. The techniques of age determination are well established and usually present only minor problems in the temperate zone. However, estimates of population size and of natural mortality, while based on well-developed theory, usually cannot be adequately validated. Most of the methods available have been developed theoretically and applied to extensive fisheries where many of the conditions affecting the estimates cannot be assessed, and where much of the basic catch and effort data is only sampled. Moreover, certain of these methods require supplementary information derived from tagging programmes in which it is often only assumed that tag loss, mortality due to tagging, and other adverse effects of the tag are not too significant.

The present paper is an examination of factors causing error or bias in the estimates of exploitation and catchability, derived from tag and recapture data, in a small intensive fishery. Such examination affords an estimation of the magnitude of the errors from which correcting factors may be derived for subsequent estimates of mortality and population size.

[1]Received for publication January 20, 1962.

[2]Abstracted from a portion of a thesis submitted in conformity with the requirements for the degree of Doctor of Philosophy in the University of Toronto.

[3]Present address: Department of Zoology, University of Hawaii, Honolulu 14, Hawaii.

J. Fish. Res. Bd. Canada, **20**(5), 1963.
Printed in Canada.

The study was conducted on a small population of maskinonge (*Esox masquinongy* Mitchill), contained in an impoundment and fished exclusively by nets operated solely for the experiment so that there was a complete knowledge of the effort expended and the catch taken. The population investigated was that in Nogies Creek, a sanctuary consisting of a small lake and 4 miles (6.5 km) of river. The data were obtained by a 9-year experimental fishery, which included extensive marking and release programmes in all years. All fishing was done by stationary trap nets and all fish netted were examined. The area is bounded above and below by dams which prevent immigration and minimize emigration, and the population may therefore be assumed closed in this respect. The study suffers from the errors associated with small numbers but statistics of catch and effort, which in larger ventures have often in part to be filled out by estimates, were directly measured.

MATERIALS AND METHODS

Nogies Creek Sanctuary (first described by Crossman, 1956) is located approximately 78°30′W Long, 44°30′N Lat, in the Kawartha Lakes region of south central Ontario. The sanctuary area (Fig. 1) consists of an 80-acre (0.32 sq km) lake, maintained by a concrete dam, and 4 miles (6.5 km) of river. Further passage of fish up the river is blocked by the ruins of a rubble dam

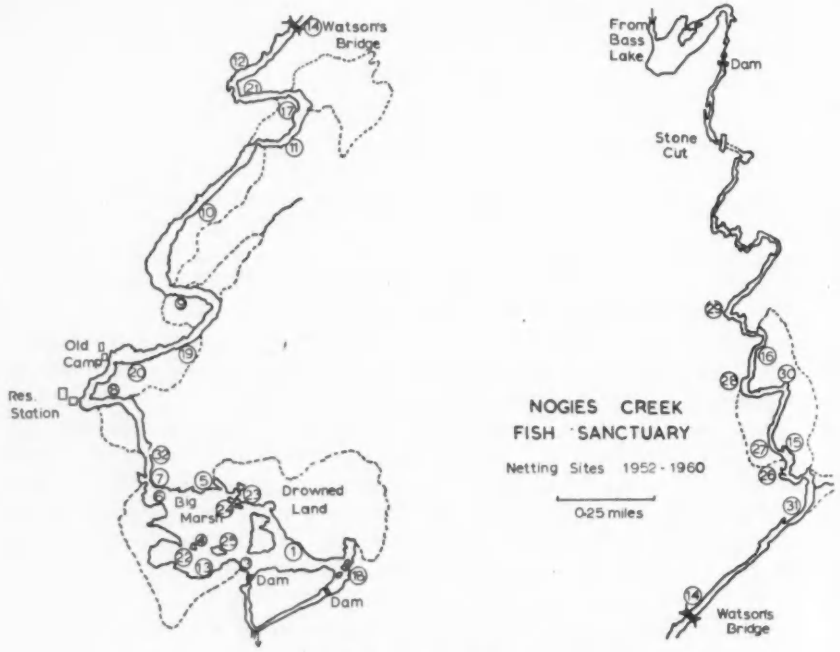


FIG. 1. Map of Nogies Creek Sanctuary showing netting sites.

through which the water percolates. The total water area is approximately 400 acres (1.67 sq km) of which an estimated 200 acres, consisting mainly of drowned land, is less than 2 feet (0.6 m) deep. The rate of flow was estimated by Crossman to be about 90 cubic feet (2.5 cu m) per second in July.

To exert a controlled fishing pressure on the Nogies Creek population, trap nets were fished each year during May and early June and again in October. The nets used were standard trap nets with 2-inch (51-mm) stretched mesh, of two sizes designed to be set in 6 and 8 feet of water, respectively. Net sites used in the study are shown in Fig. 1. Except during 1956 and 1959, fish netted in the fall were transplanted to public fishing waters. This removal from the sanctuary constituted the actual fishing mortality. Fish netted during the spring periods, and during the falls of 1956 and 1959, were tagged and returned to the sanctuary to establish a tagged population for further study. Since these fish could be re-identified, they could, in a sense, be considered to have undergone fishing mortality also.

Fish were tagged with numbered preopercular disc tags in the manner outlined by Crossman (1956). Measurements of fork length were made and recorded to the smallest quarter-inch. Six to 10 scales were removed from above the lateral line approximately midway between the operculum and the anterior base of the dorsal fin. Date, net site, and pertinent remarks such as the condition of the fish were recorded. Fish were weighed during the fall periods of 1954, 1955, and 1956. A burlap bag was immersed in water, wrung out and weighed on a dairy-type spring scale. The fish was then placed in the bag and the difference in the two weights recorded to the nearest tenth pound (45 g). Scale impressions were made on soft acetate slides with a jeweller's press and age determinations made with a Leitz "Trichinoskop" projector.

Hatchery fish, supplied by the Provincial Fish Hatchery at Deer Lake, were fin-clipped and planted as 4- to 5-inch (10–13-cm) fingerlings about the first week of July each year. The paired fins were used in rotation so that a given fin was clipped once every 4 years. Age determinations were checked against the fin-clip as positive identification for recaptures. In the present paper the recoveries from hatchery plantings are not considered.

THE TAGGING EXPERIMENT

The purpose of the tagging experiment was to set up a secondary population of known size which, as it was being exploited, could be used to estimate the total population and the mortality parameters. Provided certain conditions are met, the rate of recapture of tagged fish may be used to estimate the rate of exploitation (E) of the population. The rate of exploitation may be used to estimate the coefficient of catchability (q) which is the fraction of the population caught by a defined unit of effort. The parameters N (the total number of fish in the stock) and M (the coefficient of natural mortality) can also be estimated from the tagging experiment by indirect means.

The basic catch and effort data are given Table I. Fish were returned to the sanctuary in all spring nettings and the fall nettings of 1956 and 1959.

TABLE I. Total catches of maskinonge from Nogies Creek for the spring and fall netting periods of 1952 to 1960.

	Effort	II	III	IV	V	VI	VII	VIII	IX+	Fall catch IV+	Fall catch total
1952	S 232	25	19	50	19	19	2	1	0		
	F 90	3	18	57	30	29	9	3	0	128	149
1953	S 161	2	32	85	69	23	8	2	1		
	F 102	1	13	39	46	10	6	1	1	103	117
1954	S 136	1	13	12	12	4	4	0	1		
	F 105	8	18	51	26	24	3	0	0	104	130
1955	S 104	12	60	55	49	18	3	4	2		
	F 152	6	33	73	83	45	14	0	0	215	254
1956	S 174	2	33	62	40	48	17	1	3		
	F 153	14	45	96	65	37	18	0	1	217	276
1957	S 216	6	25	56	42	27	11	4	2		
	F 458	36	117	192	111	47	16	1	2	369	522
1958	S 204	0	18	57	27	14	3	0	0		
	F 410	156	147	71	47	12	5	2	1	138	441
1959	S 217	19	68	40	11	15	5	2	2		
	F 299	129	165	49	23	10	2	0	0	84	378
1960	S 235	5	54	111	21	14	7	1	0		
	F 237	44	113	85	29	12	1	2	0	129	286
Total	S	72	322	528	289	182	60	15	11		
	F	397	669	713	460	226	74	9	5		

They were transplanted to other waters in all other fall netting periods. The recapture data, for all fall periods are shown in Table II.

It is of utmost importance, in any tagging study, that the tag does not render the fish more, or less, catchable and that there is no tag loss or mortality due to tagging. Each of these 3 potential sources of error was particularly examined to determine its existence and whether correcting factors could be obtained.

It is believed that the tag did not seriously alter the catchability of the fish since the nets used were of heavy, fairly rigid twine and simply retained the fish after they passed through the funnel, and only accidental "gilling" of small fish occurred. However Muir (1960) reported that a marked reduction in the length increment of tagged fish occurred and ranged from about 25% (age-group IV) to about 80% (age-groups VI and VII) of that attained by untagged fish. The cause of this reduction is unknown, but it is surmised that the tag might act as a warning devide for prey.

TABLE II. Numbers of tags recaptured each fall and the seasons of release (1952–1960).

	Season of release											
	n	$n+1$		$n+2$		$n+3$		$n+4$		$n+5$	
Fall of recapture	S	S	F	S	F	S	F	S	F	S	Total
1952	18										18
1953	26	3									29
1954	9	8	3	1							21
1955	32	3	5	3	0	0	2				45
1956	43	13	0	0	2	1					59
1957	75	44	191	6	2	1	1	1			321
1958	20	6	1	5							32
1959	16	3	1								20
1960	24	17	30	4	2	0	0	1	0	1	79

It will be shown that an increase in catchability occurs with age, probably as a function of size, and since the presence of the tag reduced the growth increment, then it may have influenced catchability. Estimates of trends in catchability with age will, therefore, be made within a single netting period during which the normal growth increment would be small and errors, due to the lack of growth of the tagged fish, negligible. Such errors would be large, however, in the consideration of tags recaptured in subsequent periods. Since the numbers of recaptures of each age are not large, the data will not be corrected for differential catchability due to the reduction in growth. It is necessary to assume, therefore, that the reduced rate of growth for the tagged fish will not seriously bias the estimates of exploitation.

Tag loss and mortality due to tagging produce errors of far greater magnitude and are not so easily set aside. The following sections give particular attention to these two phenomena and to trends in catchability and movement with age to determine their influence on the data interpretation.

Rate of Tag Loss

During the course of the study it was observed that the nylon affixing the tag, when looped about the preopercular bone, rarely became firmly healed into the flesh. On some maskinonge recaptured, the loop had come so close to the surface that it was inadvertently pulled off during the normal handling and would probably have been quickly sloughed even if the fish had not been captured and handled. As the loop works its way to the surface, the resulting wound heals but produces a noticeable scar. Thus it was possible to recognize fish from which the tag been sloughed. It is likely that even if the tag had been lost due to knot failure (if such loss did not take place within the first week or so after tagging) sufficient irritation would have occurred to produce a recognizable scar. Recognition of the scars made it possible, therefore, to estimate the rate of tag loss after an initial period of 1 or 2 weeks. Such scars were routinely looked for and recorded.

The number of scars recorded and tags recaptured in each fall period are shown in Table III. No scars were recorded for the autumns of 1954 or 1955 due, apparently, to a misunderstanding on the part of the field workers in those

Table III. Summary of tags recaptured and scars observed in fall fisheries (1952–1960) and the estimated average time (in seasons) of all releases extant in each fall. The total recaptures include tags and tag scars.

Year of recapture	Total recaptured	Number of scars	Percent scars	Estimated av. time out
1952	19	1	5.2	1.0
1953	31	2	6.5	1.5
1954	21	–	–	–
1955	45	–	–	–
1956	69	10	14.5	3.3
1957	360	39	10.8	2.7
1958	47	15	31.9	4.3
1959	29	9	31.0	3.7
1960	93	14	15.1	2.6

years. The ratio of scars to scars-plus-tags ranges from 5.2% for 1952 to 31.9% for 1958. If the probability of a tag being lost increases with the length of time since tagging (time out), then the ratio of tags lost to tags retained will rapidly increase with time since tagging. Thus when there is an accumulation of fish from earlier tagging periods in the catch, the average time out determined from the tag recaptures will actually be less than the average for fish that have lost tags. The time out for all releases (tags-plus-scars) still living will be somewhat intermediate.

To determine the average time out for all releases, it was necessary to estimate the number of releases extant, in a given year, from each previous tagging season. For this purpose it was assumed (in the light of the mortality studies, in preparation) that 30% of the tagged population died of natural causes each

year. The year was divided into two periods, one from spring to fall and the other from fall to spring, both being given equal weight for time and mortality. Of the number of fish estimated to be present at the start of each succeeding half-year period, 16% (an annual mortality of 30% is equivalent to about 16% for each of the two halves) were subtracted for natural mortality. The numbers of tagged fish removed by netting were subtracted at the appropriate times and the natural mortality corrections applied to the estimated number remaining. Such consideration was confined to releases of age IV and older, since younger fish (as will be shown) were not sufficiently caught by the gear.

For example, 143 fish age IV and older were tagged and returned to the sanctuary in the spring of 1957 and an estimated 120 (16% mortality) of these remained at the start of the fall fishery. Seventy-five of these were recaptured and transplanted leaving an estimated 45 extant. By the fall of 1958 these 45 fish had been subjected to natural mortality for an additional year (30%), so that an estimated 31 releases 3 seasons old were therefore extant in the fall of 1958. Similar estimates were made for all releases possibly extant in the fall of 1958 and the average time out of these was calculated from the estimates and found to be 4.3 seasons. The calculations were not carried beyond the 9th season (4.5 years) after tagging since the estimated numbers surviving to that point were generally very small. Furthermore, since the minimum age at tagging was 4 years, all the tagged fish would be at least 8.5 years old after 9 seasons. Only a few fish were observed to exceed this age even without a tag. The truncating effect of assuming zero survival in the 10th season resulted in only a slight reduction in the estimated average time out and is considered to be inconsequential. Similar estimates were made (Table III) for all falls except 1954 and 1955, for which no scars were recorded. The data plotted in Fig. 2 provide at least a crude estimate of the rate of tag loss.

Virtually all of the tags have apparently been lost after the third year (6th season), 30% after the second year and 8.5% after the first. Only 3 fish have actually been recaptured in all periods with tags older than 3 years. A similar progressive increase in the rate of tag loss was reported by Calhoun *et al.* (1951) due to the deterioration of the plastic and metal materials used. In the present case, migration of the monofilament through the bone is believed to be the major cause of tag loss. The rate of tag loss estimated by these approximations must be considered with reservation and in the present study recaptures were disregarded after the second season.

Mortality Due to Tagging

A mortality due to the handling and tagging of fish is to be reasonably expected in this type of experiment. The approximate magnitude of such loss may be estimated by the method developed below. The method, however, estimates the total loss during the season following the tagging period, due to tagging mortality, tag loss and natural mortality, and does not provide for separation of the components. The smooth curve in Fig. 2 suggests that tag loss during the first season may be relatively constant from year to year and, as will be seen, the inclusion of the natural mortality component does not seriously

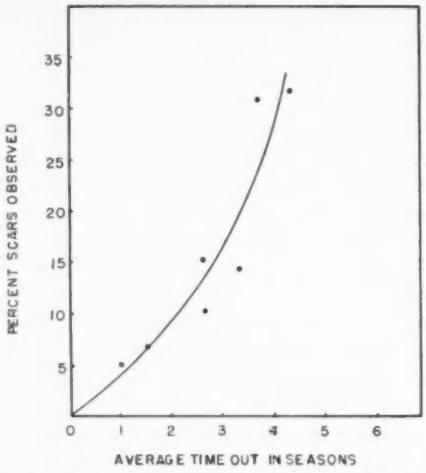


FIG. 2. Rate of tag loss. The relation between the observed percentage of scars among recaptured releases and the estimated time out of the releases extant at the time of recapture. One season is equivalent to one-half year. The line shown was fitted by eye.

hinder the application of the estimates. Since the method requires that fish be returned to the sanctuary during the fall fishery, it could be applied only to the data of 1956 and 1959.

The season of tagging, either spring or fall, is designated as period zero, and the next two seasons of recapture (fall and spring or spring and fall) as periods 1 and 2. During a tagging period — say the fall of 1956 — T fish are tagged and released and R_1 of these are recaptured and returned to the water during the following spring. The next fall R_2 are recaptured, a portion of which (R_{12}) had been seen during the spring (R_1). Obviously, the ratio R_{12}/R_1 is an estimate of the rate of recovery, in period 2, from the group of fish seen in R_1. This rate of recovery, applied to the total recaptures (R_2) should give an estimate of the total number of tags extant in period 1:

$$\frac{R_{12}}{R_1} = \frac{R_2}{s_1 T} \qquad (1)$$

where s_1 is the survival rate from period 0 to period 1, and s_1T is the number of tagged fish surviving to period 1.

Thus

$$s_1 = \frac{R_1 R_2}{R_{12} T}, \qquad (2)$$

which is the survival, after all mortality and tag loss, during the first season after tagging.

The data for spring and fall releases (age-group IV and older) of 1956 and 1959 and the subsequent recaptures are shown in the upper portion of Table IV

with the estimates of mortality for the season following the tagging period. The first season mortalities estimated for the spring and fall releases of 1956 were 25% and 9%, respectively, and for the spring and fall of 1959, 58% and 31%. In both years the spring mortalities were approximately twice as great as the fall mortalities, and mortality for both seasons was notably greater in 1959 than in 1956. The tag loss component should be about the same for spring and fall and the differences are presumably due to greater mortality from tagging, or from natural causes, during the summer than during the winter period.

TABLE IV. Estimates of mortality during the first season after tagging. See text for explanation of symbols; s_1T and s_1 are calculated from (1) and (2); m is calculated from (3).

Primary estimates for 1956 and 1959

Tagging season	T (IV+)	R_1	R_{12}	R_2	s_1T	s_1	First season mortality
Fall 1956	287	56	41	191	261	0.91	0.09
Fall 1959	87	12	6	30	60	0.69	0.31
Spring 1956	170	43	14	42	128	0.75	0.25
Spring 1959	77	16	4	8	32	0.42	0.58

Secondary estimates for 1957 and 1960

Tagging season	T	R_1	R_{12}	$1.04R_{12}$	Fall m	Spring R_1/m	First season mortality
Fall 1956 (III+)	331	66	44	46	0.70	–	–
Spring 1957 (IV+)	143	75	–	–	–	107	0.25
Fall 1959 (III+)	253	49	21	22	0.45	–	–
Spring 1960 (IV+)	155	24	–	–	–	53	0.66

The estimates for similar mortalities can be extended to two more years, 1957 and 1960. In this instance, the fall recapture of spring tags is compared to the simultaneous recapture of tags released the previous fall and the estimates are called "secondary" to distinguish them from the estimates above. Of the tags released in a fall period, R_1 will be recaptured the following spring and R_{12} of these seen again next fall. The ratio of these, R_{12}/R_1 is taken as the expected ratio for fish newly tagged in the spring and released in the fall. For example, of the fall of 1956 releases from age-group III and older, 66 were recaptured and released (as age IV+) in the spring of 1957, and 44 of these were recaptured again in the fall of 1957 (lower part of Table IV). It was assumed that 4% more were caught but not identified because of tags lost in the summer of 1957 (second season out), so that the adjusted $R_{12} = 1.04R_{12}$, and the quotient of this divided by R_1 is:

$$m = \frac{1.04R_{12}}{R_1} \qquad (3)$$

In this instance the value of (3) is $1.04 \times 44/66 = 0.70$. Of the 143 newly tagged fish released in the spring of 1957, however, only 52% (75) were recaptured in the fall of 1957. The only known difference between the 66 and the 143 released fish was that the latter group was newly tagged. The difference in recapture from the two groups may have been a result of additional mortality due to tagging or tag loss, which reduced the number effectively tagged and released to something less than 143. If the two groups were caught in the same proportion (70%), then only 107 were effectively released and 36 were lost to additional mortality in the first season. The estimated first season mortality due to tagging and tag loss is $36/143 = 0.25$. This estimate does not include natural mortality as did the "primary" estimates but as will be seen the exclusion of natural mortality during this period is probably not serious. A similar estimate for the summer of 1960 is 0.66 (Table IV).

Estimates of the total loss of tagged fish (and of tags) during the first summer may be used as corrections in the determination of the rate of exploitation by the fall fishery. However since the estimated mortalities for four different summers (1956, 1957, 1959 and 1960) ranged from 25% to 66% of the fish tagged in the spring, corrections must be derived from the individual data for each year.

Rate of Tag Recapture

The summer mortality estimates, above, represent average values for all fish from age-group IV and older. The tagging data were further examined to detect trends in the rate of recovery for the different age-groups. The numbers of tagged fish released and recaptured for each age-group are summarized in Table V; the rate of fall recapture of tags released the same spring is greater for older fish than for those from age-groups III and IV. In the first fall 7.8% of age III fish, 22.1% of age IV and 28.1% of age-group V were recaptured. The

Table V. Numbers of fish tagged and released in spring fisheries (1952–1959) and recaptured the same fall or the following spring. Fall recaptures subtracted from total to determine percentage recapture next spring.

	III	IV	V	VI	VII	VIII+
Released in spring	269	375	320	143	68	24
Recaptured in fall	21	83	90	37	18	6
Percentage	7.8	22.1	28.1	25.9	26.5	25.0
Recaptured 2nd spring	21	33	40	27	7	1
Percentage	8.5	11.3	17.4	25.4	14.0	5.6

lower recapture rate of fish from age-group III may have been due to a greater mortality or to a lower catchability compared to the older fish. During the second spring, more fish from this group were recaptured relative to the older fish, suggesting, although the numbers are small, that differential catchability

was probably in operation and more pronounced in the earlier year when the fish were a year younger.

If such were the case, then a similar, less obvious effect may have also occurred for the older fish. Considering the possibility of bias resulting from varying catchability, tag loss and mortality due to tagging, estimates of trends in catchability with age must be derived from the data of a single netting period rather than from recaptures from a second season.

Trends in Catchability with Age

Catchability, varying with size or age, for a particular gear, is often difficult to detect and even more difficult to assess. Ricker (1958) cites examples in which catchability continued to increase, declined, or leveled off with older ages. Latta (1959) showed that for several species in Michigan lakes the rate of recapture by trap nets increased with the size of the fish and biased the dependent population estimates. The problem of catchability varying with size or age must be given particular attention in the examination of catch statistics.

In the present study, adequate data were available from the fall fisheries of 1956 and 1959, to estimate the coefficient of catchability for each age-group. The method requires that the netting period be short so that recruitment and mortality be negligible. The information required consists of the number of tagged fish of each age released during the period, the number of these recaptured during the same period (only the first recapture is counted), the number of nets and the number of days fishing. These data are shown in Table VI.

Table VI. Estimates of the coefficient of catchability (q) for age-groups III, IV, V and VI+ for the Nogies Creek maskinonge during the fall netting periods of 1956 and 1959. T is the number of tags released during the fall netting period and R is the number of these tags recaptured during the same period.

	Number of days (n)	Number of nets (f)	III		IV		V		VI+	
			T	R	T	R	T	R	T	R
Fall 1956										
Number	22	7	45	4	123	18	91	18	73	17
R/(T–R)			0.098		0.171		0.246		0.298	
q			0.0012±.0006		0.0021±.0004		0.0029±.0006		0.0034±.0007	
Fall 1959										
Number	28	11	165	31	49	13	23	6	12	3
R/(T–R)			0.231		0.361		0.353		0.333	
q			0.0013±.0002		0.0019±.0005		0.0019±.0007		0.0018±.0010	
Weighted mean q			0.0013±.0002		0.0020±.0003		0.0027±.0005		0.0032±.0006	

For each age in each year, the rate of recapture, R/T (probability of recapture or "death"), may be calculated. However the transformation:

$$\frac{R/T}{1 - R/T}$$

is more useful for the following calculations. This ratio, which may also be written R/(T − R), is similar to the mortality/survival ratio which Bess (1961) terms the "odds against survival" (odds against not being recaptured). Either R/T or R/(T − R) can be expressed in terms of q, but the latter provides a mathematically easier solution.[4]

By definition, q is the fraction of the population caught (and tagged) with one unit of effort. Letting f be the number of nets fished per night, and assuming that the product fq is small relative to unity, this product is the average fraction of the population caught per night. After the first night, the proportion not tagged is $1 - fq$. Since a fraction fq of these fish are tagged the second night, the proportion remaining untagged after the second night is:

$$(1 - fq) - fq(1 - fq) = (1 - fq)^2$$

and so on; after the nth catch, the proportion untagged is $(1 - fq)^n$.

Let p_n be the fraction of the population tagged but not recaptured up to and including the nth catch. On the nth catch this fraction increases by the proportion of the population that is newly tagged, $fq(1 - fq)^{n-1}$. It decreases by the proportion previously tagged which is recaptured for the first time, fqp_{n-1}. These considerations give the linear first order difference equation:

$$p_n - (1 - fq)\, p_{n-1} = fq(1 - fq)^{n-1}$$

which has the solution

$$p_n = nfq\,(1 - fq)^{n-1}. \tag{4}$$

Let N be the original number of fish in the population, T the number tagged and R the number recaptured. Then

$$\frac{T_n}{N} = 1 - (1 - fq)^n \tag{5}$$

and

$$\frac{R_n}{N} = 1 - (1 - fq)^n - nfq(1 - fq)^{n-1}. \tag{6}$$

Thus from (5) and (6):

$$\frac{R_n}{T_n - R_n} = \frac{1 - (1 - fq)^n - nfq(1 - fq)^{n-1}}{nfq(1 - fq)^{n-1}} = \frac{(1 - fq)^{-(n-1)} - 1}{nfq} - \frac{n - 1}{n}. \tag{7}$$

But,

$$(1 - fq)^{1-n} = 1 - (1 - n)fq + \frac{(1 - n)\,(-n)}{2}(fq)^2 - \frac{(1 - n)\,(-n)\,(-n - 1)}{6}(fq)^3 + \ldots$$

Substituting this series into equation (7) and simplifying,

$$\frac{R}{T - R} = \frac{(n - 1)}{2}fq + \frac{(n - 1)\,(n + 1)}{6}(fq)^2 + \frac{(n - 1)\,(n + 1)\,(n + 2)}{24}(fq)^3 + \ldots \tag{8}$$

[4]I am grateful to Dr Harold White of the Department of Mathematics, University of Hawaii, for suggesting the following solution and for carrying out the necessary calculations.

From equation (8), the relationship between q and R/(T – R) is a curve which is characteristic of the number of days fished (n) and the number of nets used (f). The curves for 1956 ($n = 22, f = 7$) and 1959 ($n = 28, f = 11$) are plotted in Fig. 3. The values for q (Table VI) corresponding to observed values of R/(T – R) may be read from the appropriate curve in Fig. 3 or calculated from equation (8).

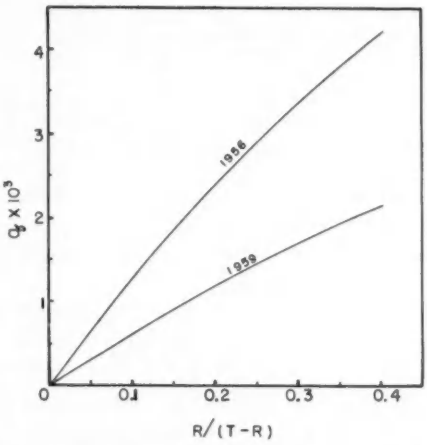


FIG. 3. The relationship between the coefficient of catchability (q) and the values R/(T–R), derived from the tagging study, described by equation (8). The equation for the 1956 curve (7 nets fished for 22 nights) is:
$R/(T-R) = 10.5(7q) + 80.5(7q)^2 + 483(7q)^3 + \ldots$
and for the 1959 curve (11 nets fished for 28 nights) is:
$R/(T-R) = 13.5(11q) + 130.5(11q)^2 + 979(11q)^3 + \ldots$

The general equation for 1956 is:

$$R/(T - R) = 10.5(7q) + 80.5(7q)^2 + 483(7q)^3 + \ldots$$

and R/(T – R) has the value 0.098 for age III, 0.175 for age IV and so on (Table VI). The values of q may be determined by substituting the observed R/(T – R), for each age at a time, and solving the equation. However the graphical solution is simpler and all ages can be solved at the same time. This solution may be obtained by selecting a series of values for q and substituting these, one at a time, into the right hand side of the equation. This provides a series of corresponding R/(T – R) and q values which may be plotted as in Fig. 3 and a smooth curve drawn. From this curve, the q values corresponding to the observed R/(T – R) for each age may be easily read.

For the 1956 general equation, for example, an arbitrary q value of 0.0030 may be selected as a start. Thus the right hand side of the equation becomes

$$0.2205 + 0.0355 + 0.0045 + \ldots$$

and the R/(T – R) is therefore 0.2605 and this (0.0030, 0.2605) is one point to be plotted on the graph. Other points are obtained by setting q equal to 0.0025, 0.0035, etc. It is probably unnecessary to take the right hand side beyond the third term since the values rapidly diminish.

The calculated values for q for each age for 1956 and 1959 are shown in Table VI. The final row of the table shows the weighted means for q obtained by the formula:

$$\frac{T_{56}\, q_{56} + T_{59}\, q_{59}}{T_{56} + T_{59}} \qquad (9)$$

The standard deviation for the q values was derived from the binomial limits on R in the following manner. The limits on R are

$$R \pm \sqrt{T \cdot \frac{R}{T}\left(1 - \frac{R}{T}\right)}$$

and, dividing by T – R, the limits on R/(T – R) are

$$\frac{R}{T-R} \pm \sqrt{\frac{R}{T(T-R)}}$$

These limits were located on the curve (Fig. 3) and those for q were read from the ordinate. Although this method assumes that q is constant for each age (which is improbable) the estimates of standard deviation give some indication of the degree of confidence involved.

The estimated q values for 1956 increase from 0.0012 at age III to 0.0034 at age VI+, but the values for 1959 remain constant at 0.0019 after age IV. The mean values for the two years increase, almost linearly, from 0.0013 for age-group III to 0.0032 for age-group VI+; these values, however, are greatly influenced by the large catches in 1956. That catchability varies between ages and between years is quite apparent but the reason for the diffrences between years can only be surmised. The marked difference in the age structure of the two populations is the most likely source of the disagreement, either as sampling error or as an actual influence on catchability.

In the final section of this paper it is necessary to consider the average coefficient of catchability for all fish age IV and older. An estimate for such a value may be obtained here by using a weighting formula similar to (9) and including all the required age-groups in both years. The average coefficient of catchability for age IV+ is 0.0025, and for V+ is 0.0030. The similar values derived from the 1956 data alone are 0.0027 and 0.0032, respectively.

Since the mesh was capable of retaining most fish from age-group II, and probably all from age-group III, it is unlikely that the observed trend reflects mechanical selection in the nets. Furthermore, since the entire sanctuary was netted, general immigration of younger fish was essentially out of the question. However if the tendency to move, or the distance moved, increases with age then the fishing area for a single net would appear to increase also and a localized

immigration into the area of the net (within the closed population) might be observed. Such hypothesis suggests that older fish move further or more actively than the younger fish and that there is a critical distance between nets for the adequate sampling of each age-group. Watt (1959) reached a similar conclusion by comparing the recaptures by nets and by anglers. Since his data were obtained from two types of gear, he could not derive direct correction factors. The coefficients of catchability determined from the present tagging experiment are directly applicable to the general catch data which were obtained by the same gear.

Movement of Tagged Fish

The fall recaptures of spring tags for the years 1956 to 1960 were examined for trends in distance travelled. It was found that older fish tended to show a greater distance between sites of release and recapture, and that a greater percentage of younger fish were caught in the same net both times. Since the numbers in each age-group were small, only two categories of distance travelled could be considered.

The recaptures by age, shown in Table VII, were stratified by movement less than 0.5 mile (0.8 km) and greater than 0.5 mile between the sites of release and recapture. Forty-four percent of the recaptures from age-group VI+ and only 27% from age-group III were taken by nets greater than 0.5 mile from the

Table VII. Fall recaptures (1956–1960) of fish tagged the previous spring, grouped by age and distance between tagging and recapture sites. Data augmented by double recaptures from previous tagging.

	Age-group							
	III		IV		V		VI+	
Year	0.5– mile	0.5+ mile	0.5– mile	0.5+ mile	0.5– mile	0.5+ mile	0.5– mile	0.5+ mile
1956	6	0	17	3	9	5	5	6
1957	0	1	21	9	32	16	16	14
1958	3	0	5	2	2	3	2	3
1959	4	1	3	1	3	0	2	4
1960	3	4	25	5	7	0	9	0
Total:	16	6	71	20	53	24	34	27
Percentage:	73	27	78	22	69	31	56	44

Distance		III	IV	V	VI+	Total
Less than 0.5 mile	*f*	16	71	53	34	174
	F	15.25	63.08	53.38	42.28	
More than 0.5 mile	*f*	6	20	24	27	77
	F	6.75	27.92	23.62	18.71	
Total:		22	91	77	61	251

$\chi^2 = 8.65$, d.f. = 3, $p = 0.035$.

point of release, indicating that older fish tend to travel greater distances. Tested for significance in a 2 by 4 contingency table, the data yielded a χ^2 of 8.65 with 3 degrees of freedom and a probability of 0.035. The observed trend in distance travelled with age is reasonably significant in view of the extent to which the data were pooled.

Fish tending to move greater distances would encounter more nets and have a greater probability of being caught. Localized "immigration", as a function of movement, is a reasonable explanation of the trend in apparent catchability with age. Such explanation, that the "sweep" of the nets increases with the mobility of the fish, has been offered before (e.g. Watt, 1959).

Estimates of Exploitation and Catchability

A consideration of the many sources of error has shown that estimates of the rate of exploitation (E) from the recapture data will be seriously biased unless a correction for tagging mortality and tag loss is applied. The numbers of spring releases and fall recaptures for each year are shown in Table VIII. Corrections for the estimated summer mortality for 1956, 1957, 1959 and 1960 were applied to estimate the numbers of tags extant in the fall, and the rates of exploitation determined by the rates of recapture of these tags. Uncorrected rates of recapture for the remaining years are also shown and are used for supplementary information.

Table VIII. Estimates of the rate of exploitation from the fall recapture of spring tags. Values in parentheses are rates of recapture for years in which the loss of tagged fish could not be estimated. Estimated summer mortality values taken from Table IV.

Year of catch	Released in spring	Estimated summer mortality	Estimated extant in fall	Recapture in fall	Rate of exploitation E	$-\log_e(1-E)$	Total effort in fall
1952	90	–		18	(0.20)	(0.22)	90
1953	186	–		26	(0.14)	(0.15)	102
1954	32	–		9	(0.28)	(0.33)	105
1955	127	–		32	(0.25)	(0.29)	152
1956	170	0.25	127	43	0.34	0.42	153
1957	143	0.25	107	75	0.70	1.20	458
1958	86	–		20	(0.23)	(0.26)	410
1959	75	0.58	32	16	0.50	0.69	299
1960	154	0.66	53	24	0.45	0.60	237

The relationship between the rate of exploitation and mortality, when the season is short so that natural mortality can be ignored, is stated by equation (5) (T represents the catch and N the total population):

$$T/N = E = 1 - (1 - qf)^n.$$

But since qf is small, $(1 - qf)$ is approximated by e^{-qf} and we may write:

$$E = 1 - e^{-nqf}.$$

Since f is the average number of nets fished per night and n is the number of nights, we may simplify by letting f represent nf which is the total net nights fished during the period.

Rearranging and taking logarithms, we get:

$$-\log_e (1 - E) = qf. \qquad (10)$$

From equation (10) it may be seen that if $-\log_e (1 - E)$ is plotted against f, a straight line should be obtained which passes through the origin and the slope of which is q.

The values of $-\log_e (1 - E)$, taken from Table VIII, are plotted against the fishing effort for the corresponding years in Fig. 4. The line shown was fitted to the four corrected points by a least squares regression. The calculated values for the slope and intercept are 0.0026 and −0.0085, respectively, the intercept being in excellent agreement with the theoretical value of zero.

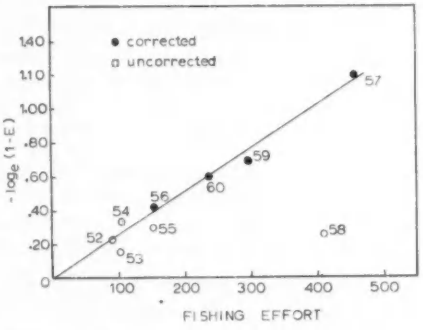


FIG. 4. The relation between instantaneous fishing mortality ($-\log_e (1-E)$) and fishing effort, as determined by the recapture of spring tags in the fall fisheries. The line shown was calculated for the corrected points only. Corrections accounted for the loss of tagged fish during the summer.

In addition the intercept agreeing with that predicted by theory, the estimate of the average coefficient of catchability for age-group IV and older (slope of the line, 0.0026, is q) agrees with the similar estimate (0.0025) derived from the within-season recapture of tags. These two estimates of q are independent, the one being derived from the fall recapture of spring tags after correction for summer mortality and tag loss, and the other derived from the simultaneous tag and recapture of fall tags.

It is noteworthy that the uncorrected points for 1952, 1953, 1955 and 1958 fall below the line. Corrections for summer mortality increase the estimates of the rate of exploitation and would bring these points closer to the line. The data for 1954 are too sparse to warrant much confidence.

The customary assumption, that tag loss and mortality due to tagging are negligible, is invalid for the Nogies Creek maskinonge. However, the mortality corrections appear to overcome this and render the tagging data useful for subsequent mortality studies. Furthermore, the often necessary assumption that catchability does not vary with age is also invalid. It appears from the above study that adequate inspection of the assumptions requires data which are not normally available from routine tagging programmes. Unfortunately, it may be possible to obtain such data only from small controlled fisheries.

ACKNOWLEDGMENTS

This study was carried out as a joint project with financial assistance and direction from the University of Toronto, the Ontario Department of Lands and Forests, and the Toronto Anglers' and Hunters' Association. I am deeply indebted to Dr F. E. J. Fry, as chairman of the project committee and as my graduate supervisor, for his guidance and encouragement throughout the study.

The collection of data was possible only with the assistance of numerous undergraduate assistants and employees of the Ontario Department of Lands and Forests.

REFERENCES

BESS, H. A. 1961. Population ecology of the gypsy moth *Porthetria dispar* L. (Lepidoptera: Lymantridae). *The Connecticut Agricultural Experiment Station, Bull.* No. 646, 43 pp.

CALHOUN, A. J., D. H. FRY, JR. AND E. P. HUGHES. 1951. Plastic deterioration and metal corrosion in Petersen disk fish tags. *California Fish and Game*, **37**(3): 301–314.

CROSSMAN, E. J. 1956. Growth, mortality and movements of a sanctuary population of maskinonge (*Esox masquinongy* Mitchill). *J. Fish. Res. Bd. Canada*, **13**(5): 599–612.

HOLT, S. J., J. A. GULLAND, C. TAYLOR AND S. KURITA. 1959. A standard terminology and notation for fishery dynamics. *J. Conseil Expl. Mer.*, **24**(2): 239–242.

LATTA, W. C. 1959. Significance of trap-net selectivity in estimating fish population statistics. *Papers Michigan Acad. Sci., Arts and Letters* for 1958, **44**: 123–138.

MUIR, B. S. 1960. Comparison of growth rates for native and hatchery-stocked populations of *Esox masquinongy* in Nogies Creek, Ontario. *J. Fish. Res. Bd. Canada*, **17**(6): 919–927.

RICKER, W. E. 1958. Handbook of computations for biological statistics of fish populations. *Bull. Fish. Res. Bd. Canada*, No. 119, 300 pp.

WATT, K. E. F. 1959. Studies on population productivity. II. Factors governing productivity in a population of smallmouth bass. *Ecological Monographs*, **29**(4): 367–392.

Factors Influencing the Effectiveness of Fresh Fish Washing Operations[1,2]

By W. A. MacCallum

Fisheries Research Board of Canada
Technological Unit, St. John's, Nfld.

AND

M. W. Mullan and Isabel N. Plaunt

Department of Fisheries of Canada
Fish Inspection Laboratory, Halifax, N.S.

ABSTRACT

The effects of ratio of the amount of fish to that of wash water, kinetic energy of impinging water, method of water application and concentration of available chlorine in the wash water on the washing of eviscerated fresh cod of various caught-ages were studied. The studies were designed to provide information of practical value to engineers interested in designing machines to wash slime and bacteria from fish received at filleting plants. A quantitative relation between kinetic energy of impinging wash water and fish to water ratio was established for one practical type of spray washing equipment. Effective spraying was found to be more efficient than fluming or dipping. However, fish dipped several times in water deposited less bacterial load on a clean surface than fish washed effectively on the skin side only by a jet of water. Thus, washing out the body cavity was found to be important. Caught-age was found to influence the results *only* for washing methods of relatively low effectiveness, namely in fluming and in washing inefficiently with a jet or spray of water. Ineffective spray washing was shown to be associated with waste of equipment and high costs while serving no useful production purpose. Highly effective methods of spray washing fish of all caught-ages were shown to be suitable for efficient application in fish filleting and skinning lines. Free chlorine concentrations as high as 100 ppm in the wash water did not increase washing effectiveness as measured by a bacteriological method.

INTRODUCTION

That bacteria present in and on freshly caught fish multiply while the fish are stowed on fishing boats and are transferred from fish to freshly cut fillets during operations at filleting plants, were early findings in the modern science of fillet production (Castell, 1947). Also, Castell (1953) demonstrated that washing fish before filleting reduces the transfer of bacteria from fish to fillet and thereby extends the keeping time of the fillet. Tarr and Lantz (1949) reported on the effectiveness of washing fish by certain mechanical devices.

Today, in virtually all filleting plants in eastern Canada, fish are washed before being filleted, and in most plants some mechanical means of washing is

[1]Received for publication December 27, 1962.

[2]The authors of this paper have contributed equally in this joint project, the results of which were reported at the 5th Atlantic Fisheries Technological Conference, Williamsburg, Virginia, February 19–22, 1961.

J. Fish. Res. Bd. Canada, **20**(5), 1963.
Printed in Canada.

used. However, the force and rate of water application, and other possibly influential factors vary widely from plant to plant; design of the various washing arrangements having been guided more by what was easily attained than by definite knowledge of the influence of different factors on the effectiveness of the washing operation. Mullan *et al.* (1958) found that fish-washing methods in commercial use varied widely in effectiveness. As measured by a bacteriological method, washing effectiveness was found to reach 99% regularly in a few plants while 70% was the greatest effectiveness achieved in others.

The studies reported here were undertaken primarily to determine the influence of certain physical factors on the effectiveness of fish washing and thereby facilitate the designing of washing equipment. The factors studied were (1) the work done by the water on the fish to remove slime, (2) the rate of water application, and (3) means of water application. The effects of certain concentrations of free available chlorine in the wash water on the effectiveness of washing were also investigated. The influence of caught-age of the fish on washing effectiveness was studied as well.

These investigations were commenced in 1957 by personnel of the Fisheries Research Board of Canada, Technological Station, Halifax, N.S., and were expanded in May 1959 when bacteriologists of the Department of Fisheries of Canada, Fish Inspection Laboratory, Halifax, joined the work team.

As used in this paper, the term *effectiveness of washing* has one of two connotations. It is used to express (1) percentage of initial bacterial load removed from the skin surface of the fish by the washing operation (thus it expresses percentage reduction in contamination potential of this load), and (2) the reduction in contamination potential which washing brings about on the concentration of bacteria in drainage fluids from the fish. The first value is obtained by the direct contact sampling procedure, the second by the drainage count procedure. The procedures are described below under bacteriological methods. *Work done by the wash water* is expressed in units of kinetic energy (KE) per unit time per unit area of conveyor belt, (ft-lb/min/sq inch). *Rate of water application* is expressed as Q pounds of fish washed per gallon (Imperial) of water required to wash all exterior surfaces of each fish.

METHODS AND EQUIPMENT

Trawler-caught market cod, eviscerated and iced at time of capture, were subjected to experimental washing treatments at various caught-ages. The effectiveness of the treatments was assessed by determining the number of bacteria present on the exposed surface of the fish and in the drainage fluids before and after treatment.

Washing Methods

Spray washing. Stainless steel "Veejet"[3] nozzles which produce a sharp, flat, hard-hitting spray when directed downwards were used. Two parallel

[3]Spraying Systems Co., 3201 Randolph St., Bellewood, Ill., U.S.A. Nozzle No. ¼U6520. (Mention of manufacturers' products should not be taken as an endorsement of these products by the Fisheries Research Board of Canada.)

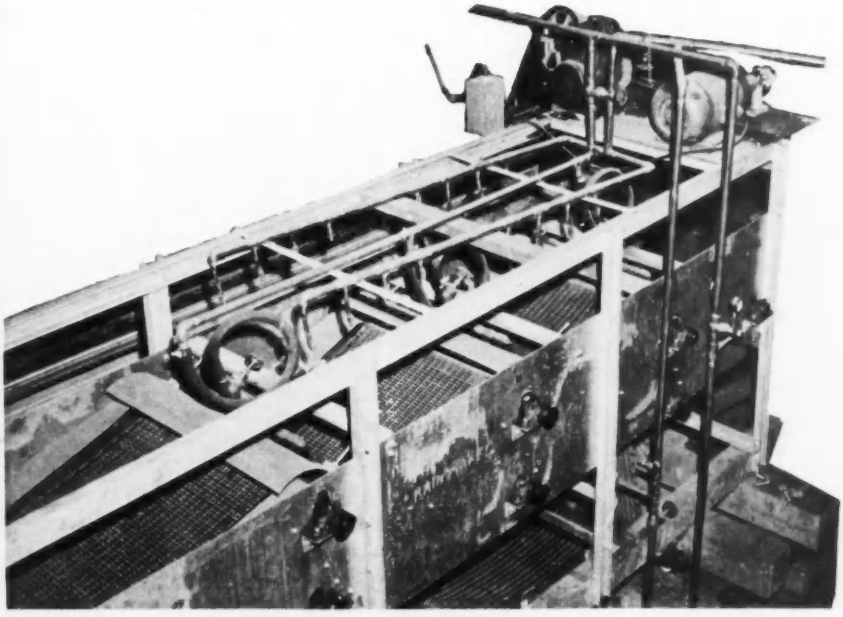


FIG. 1. A view of the experimental machine used to convey cod under a water spray. The belt travels from the reader's left to right.

rows (12 inches apart) of nozzles were placed 19 inches above and 7½ inches below the top and bottom sides of a continuous flat-wire conveyor belt[4] (½ × 1 inch mesh) of No. 302 stainless steel. A variable pitch drive[5] consisting of one mechanically operated variable pitch pulley, and one spring operated variable pitch pulley was connected to a 2-hp, 1800-rpm motor and in turn drove a Crofts[6] 70:1 reduction gear. The latter was connected to the conveyor drive sprocket by means of a roller chain drive (½-inch pitch). The conveyor drive sprocket was mounted on the same shaft on which five 4-inch diameter cast iron cast-tooth sprockets were mounted. The teeth of the latter sprockets meshed with the openings in the wire belt. In the experiments the speed of the conveyor belt was changed over a range of about 5 ft/min to 64 ft/min. Figure 1 shows the machine used to obtain the experimental data.

Thirteen nozzles on 8-inch centres were placed in each branch of the top and bottom banks. The quantity of city water used per pound of fish washed could be varied by regulating the number of nozzles, the pressure of the water and the speed of the belt. The quantity of water used was metered. Physical constants and quantities pertaining to the arrangement and use of the apparatus together with manufacturer's data for the nozzle permitted the calculation of kinetic energy exerted by the spray per minute per square inch of surface at any chosen distance above and below the nozzles. The effect of gravity on the velocity of the water at points above and below the belt has been included in the figures shown in the results. No value has been placed on the possible contribution of water rebounding from the surfaces and impinging on the fish a second time nor on the interference effect of rebounding water on primary spray.

HANDLING FISH UNDER THE SPRAY. Gutted, heads-on cod were laid by hand across the conveyor belt, side down, and were carried under and/or over the jets by the belt, being removed by hand for sampling after passing the last active jets. Values of Q were determined assuming a belt load of 10 lb per lineal foot of belt. In commercial practice, a satisfactory arrangement for distributing the fish on the belt in one layer at about this density would be required. A one-layer arrangement is recommended as it lends itself to turning each fish so that both sides are washed effectively and the fish do not drain on one another. Unfortunately one-layer washing is seldom if ever witnessed in fish plants, the tendency being to lift fish in elevator-washers where the fish are bulked several layers deep under the sprays. With the latter arrangement one can only be sure that the top side of the topmost fish is washed effectively. The elevators are operated sporadically and fish are delivered in batch lots to the cutters where recontamination of washed surfaces can occur. The bulk-washing method could be changed readily to the one-layer arrangement with no loss in plant throughput.

DIP-WASHING AND FLUME WASHING. A shallow rectangular 5-gal tray with a hoppered bottom, fitted with a large drain at the low point was used for

[4]Canners Machinery Ltd., Simcoe, Ontario, Canada.
[5]Gerbing Roto — cone drives — Renold Chains Canada Ltd., Toronto, Canada.
[6]Crofts reduction gears, Renold Chains Canada Ltd., Toronto, Canada. Reduction gear No. 4.25.

dip-washing individual fish and for fluming experiments. The tray was drained, hosed and refilled with clean city water each time a fish was dipped. The fish were dip-washed by hand, each fish being held by the head and tail and fully immersed in and withdrawn from the water. Either or both the back and underside of the fish was forced into the water the required number of times. In the simulated fluming method, a hose carrying city water was clamped to the edge of the tray and the drain from the tank was opened. The water was allowed to flow into the tray at a rate of 10 gal/min and out through the bottom drain and over the top edges of the tray. For each test three fish were placed in the tray, exposed to the flow as described for 3 min, then removed.

HOSING. As reported below, the difference in the bacterial load deposited by fish washed on the skin surface and hosed in the gut cavity and that deposited by fish washed on the skin surfaces only, was studied. The gut cavities were hosed by directing city water from a hose at a rate of 6 gal/min into the gut cavity for 1 to 5 seconds.

FISH SUPPLY. Trawler-caught market cod, eviscerated and iced at time of capture, were used in all experiments. The fish, at a temperature of about 32°F (0°C), and having a range in caught-age of 1 to 10 days, were removed from the trawler and placed in wooden boxes freshly lined with waxed paper with only sufficient small ice to retain the low temperature until washing was commenced.

BACTERIOLOGICAL METHODS

The *direct contact procedure* was designed to yield bacterial counts which would serve as indices of the amount of bacterial contamination which could be transferred directly from the skin surface of fish to absorbent surfaces such as the top of filleting boards. In this procedure a No. 1 Whatman filter paper disk, 40 cm^2 in area, was placed on the lateral surface of the skin of the fish near the tail[7], stroked with tweezers to ensure complete contact, then removed with the tweezers and placed in 120 ml of sterile 0.1% peptone solution. Subsequently this mixture was shaken 100 times in order that the disk would break and become dispersed uniformly through the solution. Suitable dilutions of the mixture were then prepared, and measured amounts of these were mixed with sterile melted Frances Dyer Agar (Dyer *et al.*, 1946) in petri plates, for bacteriological analysis by the standard colony count technique (incubation at 25°C for 4 days). The bacterial counts obtained were expressed in numbers removed from the fish per square centimeter of skin surface, although it was recognized that not all of the bacteria removed could grow under the conditions of the colony count test.

In comparing the effect of changes made in the washing method (e.g. changes in kinetic energy per minute exerted per unit area of skin surface by the spray) when bacterial counts were made by the direct contact procedure, an area near the tail of each unwashed fish was pressed and the filter paper prepared for counting. The fish was then washed immediately and an area adjacent to the first area was pressed and a sample prepared for counting. For each caught-

[7]It had been determined previously that variation in bacterial count from one fish to another in any lot was less at this location than at others tested.

age and for each variation in treatment, multiple runs were conducted, during each of which about 8 individual fish were sampled before and after washing.

The *drainage count procedure* was designed to serve as an index of the concentration of bacteria in drainage fluids from fish. It differed from the direct contact procedure only in that in the latter the filter disk, instead of being placed on the skin of the fish, was saturated in fluid which had drained from the fish onto waxed paper during a 2-min period. The bacterial counts obtained were expressed as numbers per square centimetre of filter disk, which represented some (not calculated) volume of drainage fluid.

In this procedure, different fish or different sides of the same fish had to be used for before and after washing counts, otherwise the precision of the procedure would have been reduced. For each caught-age, and for each variation in treatment, multiple runs were conducted, during each of which 10 individual fish or fish sides were sampled in the prewashed condition and 10 other fish or alternate sides were sampled after washing.

Statistics

Statistical tests for significance of differences, results of which are shown in the text and the bottom of several Tables, were by the method of paired variates.

RESULTS AND DISCUSSION

Spray Washing, Assessed by "Direct Contact" Procedure

Spraying from above and below the conveyor belt

Washing effort on uppermost side of belt was characterized as follows: KE = 2.8: Q = 13.8. Washing effort on lower side of belt was characterized as follows: KE = 3.7: Q = 7.1.

Although almost double the amount of water was applied and with much greater energy to the underside of the belt than to the upper side, for seven lots of fish, the up-spray averaged only 89% in washing effectiveness while the down-spray averaged 98%. The difference was significant at a level where P = only slightly more than 0.05. The difference is probably attributable to the presence of the mesh belt between the up-spray and the fish.

Interrelation of fish/water ratio (Q) and energy (KE) of water application in spray washing

A series of tests were carried out to investigate the interrelation of Q and KE on the effectiveness of washing. Various combinations of Q values ranging from 8.5 to 75.2 and KE values from 1.6 to 20 were studied. The results show that there is little effect from making small changes in KE and Q (Q being at the low end of the range tested).

At the P = 0.10 level no significant difference in washing effectiveness was found between KE = 1.6: Q = 14.8 and KE = 3.6: Q = 16.5 when these ratios were compared on four lots of fish. However, large changes in KE with modest changes in Q (Q being at the centre of the range tested) had a significant effect (P = 0.05). When values of KE = 1.6: Q = 27.1 and KE = 20.0: Q = 37.6

TABLE I. Effect of washing treatment on the bacteria load on various lots of fish (in this and subsequent Tables in this paper, Q = fish/water ratio, KE = work done by the water.)

	Average effectiveness[a] Treatments			
Lot No.	E KE = 20.0 Q = 37.6	G KE = 20.0 Q = 75.2	D KE = 1.6 Q = 27.1	F KE = 1.6 Q = 54.2
	%	%	%	%
49	99.2	92.7	95.1	81.3
50	99.4	98.4	98.7	93.2
51	99.5	97.4	93.0	78.3
52	99.6	98.4	98.9	93.4
53	99.1	98.6	98.8	97.1
Overall averages:	99.4	97.1	96.9	88.6

Difference E–D is significant at P = 0.05 level
Difference E–F is significant at P = 0.05 level
Difference G–F is significant at P = 0.05 level
Difference G–D is not significant at P = 0.10 level
Difference E–G is significant at P = 0.10 level
Difference D–F is significant at P = 0.05 level

[a]Percent decrease in bacteria load as assessed by direct contact method.

TABLE II. Effect of washing treatment on the bacteria load on various lots of fish.

	Average effectiveness[a] Treatments			
Lot No.	H KE = 6.4 Q = 8.5	I KE = 6.4 Q = 17	J KE = 6.4 Q = 34	K KE = 6.4 Q = 49
	%	%	%	%
54	99.5	99.2	98.7	98.1
55	99.8	99.2	98.7	98.6
56	99.7	99.6	99.1	97.2
57	98.8	98.2	96.1	98.2
58	99.3	97.5	98.0	96.4
59	97.6	97.7	97.6	97.1
Overall averages:	99.1	98.6	98.0	97.6

Difference H–I is significant at P = slightly more than 0.10 level
Difference H–J is significant at P = 0.05 level
Difference I–K is significant at P = 0.05 level
Difference H–K is significant at P = 0.05 level

[a]Percent decrease in bacteria load as assessed by direct contact method.

were compared on 10 lots of fish, the latter proved more effective showing an average effectiveness of 98.5% whereas an average effectiveness of 96.4% was obtained for the former ratio.

Table I contains data showing the significant effect of making large changes in KE with modest changes in Q (Q being at the centre and high end of the range tested). This is shown by the significance of differences E–D, E–F and G–F. Results from changing Q (Q being at the centre and high end of the range tested), KE being constant, were much less significant. This is shown by the significance attached to differences E–G and D–F (Table I). Of the treatments E, D, G, F used on the five lots of fish, E (KE = 20.0: Q = 37.6) proved more effective than D (KE = 1.6: Q = 27.1), G (KE = 20.0: Q = 75.2) and F (KE = 1.6: Q = 54.2). Treatments D and G appeared to be approximately equal in effectiveness while F, with an average of 88.6% proved to be the least effective.

When the work done by the water on the surface of fish was kept constant (KE = 6.4) and the fish/water ratio was varied through Q = 8.5, 17, 34 and 49, (Q being at the centre and lower end of the range tested), effectiveness levels attained were respectively 99.1, 98.6, 98.0 and 97.6%. As shown more fully in Table II these differences in effectiveness, although small, showed a remarkable degree of consistency from lot to lot.

The results of the above experiments are illustrated in Fig. 2, showing that washing treatments can be placed in groups on the basis of washing effectiveness. The graphs show a joint influence of fish/water ratio and work on the effectiveness of washing fish by spray methods.

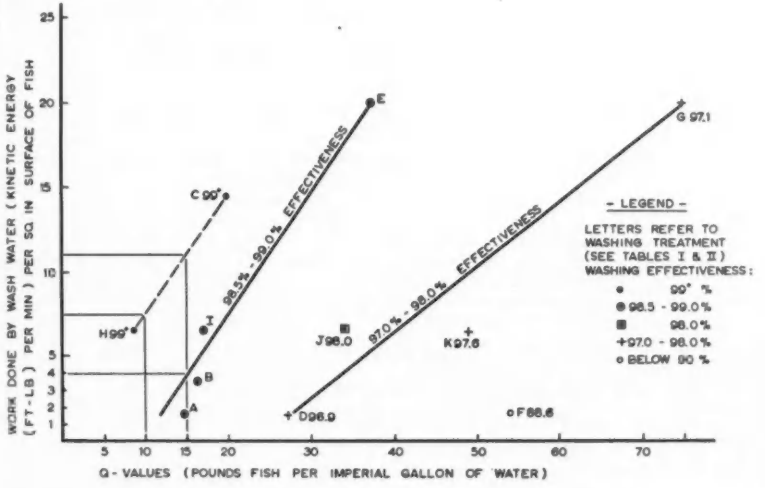


FIG. 2. Washing effectiveness promoted by various combinations of work and fish/water ratio (conversion factors: 1 ft-lb/min = 13.8 × 10^{-2} kg-m/min; 1 inch^2 = 6.45 × 10^{-4} m^2; 1 Imp gal = 4.54 l).

Influence of caught-age of the fish on effectiveness of spray washing

There is a strong suggestion in the results of the spray washing experiments that caught-age may influence the effectiveness of treatments in the lower effectiveness range associated with high Q values and low values of KE. Fish of very low caught-age (1–2 days) may not yield as high a percentage of their initial bacterial load, when washed under conditions providing a high Q and low KE, as do fish of greater caught-age (Table IIIA). This should not be too important in practice since methods yielding only high washing effectiveness should be used. At low values of Q, which as pointed out in the following discussion could be attained easily in plant operations, caught-age does not appear to have an effect on washing effectiveness (Table IIIB).

Table IIIA. Washing effectiveness obtained on fish of various caught-ages, by treatments E, G, D and F.

			Washing effectiveness[a] Treatments				
Lot No.	Caught-age	Initial bacteria count/sq cm	E KE = 20.0 Q = 37.6	G KE = 20.0 Q = 75.2	D KE = 1.6 Q = 27.1	F KE = 1.6 Q = 54.2	Difference E–F
	days		%	%	%	%	%
52	6	1,400,000	99.6	98.4	98.9	93.4	6.2
53	6	560,000	99.1	98.6	98.8	97.1	2.0
50	2	870,000	99.4	98.4	98.7	93.2	6.2
49	1–1.5	96,000	99.2	92.7	95.1	81.3	17.9
51	1–1.5	230,000	99.5	97.4	93.0	78.3	21.2

[a]Percent decrease in bacteria load as assessed by direct contact method.

Table IIIB. Washing effectiveness obtained on fish of various caught-ages, by treatments H, I, J, K.

			Washing effectiveness[a] Treatments				
Lot No.	Caught-age	Initial bacteria count/sq cm	H KE = 6.4 Q = 8.5	I KE = 6.4 Q = 17	J KE = 6.4 Q = 34	K KE = 6.4 Q = 49	Difference H–K
	days		%	%	%	%	%
54	8–10	1,900,000	99.5	99.2	98.7	98.1	1.4
57		760,000	98.8	98.2	96.1	98.2	0.6
58	3–4	61,000	99.3	97.5	98.0	96.4	2.9
59		160,000	97.6	97.7	97.6	97.1	0.5
55	1	170,000	99.8	99.2	98.7	98.6	1.2
56		80,000	99.7	99.6	99.1	97.2	2.5

[a]Percent decrease in bacteria load as assessed by direct contact method.

Influence of Various Washing Methods on the "Drainage Count" of Bacteria from Eviscerated Fish

The results of a series of washing experiments given in Table IV show the following:

(i) Hosing the abdominal cavity before spraying the exterior lateral surfaces reduced the drainage count of bacteria from the washed fish by 76–89%.

(ii) Dipping fish twice before spray washing their exterior lateral surfaces reduced the drainage count of bacteria from the washed fish by 62–63%.

(iii) The drainage count from fish dipped four times was 59–78% lower than that from fish dipped twice and then spray-washed.

(iv) The drainage count from fish dipped twelve times was 60% less than that from fish dipped four times.

Table IV. "Drainage counts" of bacteria from various lots of fish washed as follows: L — Spray washed on both exterior lateral surfaces (KE = 20.0; Q = 37.6); M — Abdomen hosed, then fish spray washed as in L; N — Fish dipped twice, underside down in 5 gal water, then sprayed as in L; O — Fish dipped four times, twice underside down, twice underside up in 5 gal water; P— Fish dipped 12 times, six times underside down, six times underside up in 5 gal water.

Lot No.	Treatment	"Drainage count" of bacteria from washed fish	Standard error of mean	Difference between treatments
				%
33	L	1,200,000	220,000	89.2
	M	130,000	28,000	
35	L	140,000	22,000	75.7
	M	34,000	10,000	
34	L	43,000	6,000	62.6
	N	16,000	2,000	
36	L	99,000	20,000	61.6
	N	38,000	15,000	
37	N	34,000	6,000	58.8
	O	14,000	5,000	
38	N	81,000	21,000	77.7
	O	18,000	5,000	
39	O	20,000	2,000	60
	P	8,100	1,800	
41	O	35,000	12,000	60
	P	14,000	5,500	

Dip Washing Treatments Compared by Both "Direct Contact" and "Drainage Count" Methods on Six Lots of Fish

Results are given for washing treatments listed below:

P — Fish dipped twelve times in 5 gal water, six times underside down, six times underside up.

R — Fish dipped twice in 5 gal water, underside down.

The average effectiveness of treatment P as assessed by the direct contact method was found to be 79%; while that of method R was found to be 46% (Table V). Average gain in effectiveness per dip for last 8 dips was 3.3%. The average effectiveness of treatment P as assessed by the drainage count method was found to be 95% and that of R, 63%. Average gain per dip for last eight dips was 3.2%.

One notes inconsistencies and low values of washing effectiveness (treatment P — direct method) in comparison to spray-washed fish on which counts were made by the same method. It would appear nevertheless from the previous section that one would expect fish given treatment P would contaminate a cutting board less than fish spray washed to attain a very high (98.5%) washing effectiveness (as measured by direct contact on the skin).

Again, there is some indication in the results of this series of experiments that fish of very low caught-age may retain a greater percentage of their initial bacterial loads when washed by dipping methods than do fish of greater caught-age (Table V).

Table V. Washing effectiveness, as assessed by direct contact method, and that, as assessed by the drainage count method, obtained on fish of various caught-ages, by treatment P (twelve dips, underside down six times, and underside up six times, in 5 gals of water) and by treatment R (two dips, underside down in 5 gals of water).

		Initial bacterial counts		Effectiveness			
				Treatment R		Treatment P	
Lot No.	Caught-age	Direct count	Drainage count	Direct method	Drainage method	Direct method	Drainage method
	days			%	%	%	%
42	7–8	2,600,000	2,600,000	69	92	95	99
47	6	1,600,000	780,000	6	72	65	88
46	5	6,500,000	5,300,000	97	95	98	96
45	3	2,700,000	2,100,000	33	60	65	95
44	3	740,000	350,000	43	0	74	98
43	2	530,000	480,000	27	58	76	93
			Average:	46	63	79	95

Chlorination

The presence of 20 ppm of free available chlorine in the wash water was not found to add to the effectiveness of twelve-dip washing, nor was the presence of 100 ppm of free available chlorine in the wash water found to increase the

effectiveness of either spray or flume washing. Effectiveness in all cases was determined by the direct contact method (Table VI).

Related Data on Haddock and Flounder

Results agree with data obtained by W. A. MacCallum and R. Gillespie (1953, unpublished data) who found that bacterial populations were removed with about the same effectiveness from the newest- and oldest-caught haddock landed from trawlers. When haddock were washed under an effective spray, the data shown in Table VII were obtained. The same workers obtained comparable results when flounders were tumbled in a wide-mesh rotary washer under a deluge of water (Table VIII). Castell (1953) showed that percentage bacterial reductions on *fillets* as a result of washing round fish by various means were low for recently caught iced fish and relatively high for fish which had been in ice for several days. Bacterial counts were made under different circumstances and after the fish had undergone different treatments than in the work reported here and it is impossible to correlate results.

Table VI. Bacterial counts, as determined by the direct contact method, before and after the fish were washed, various treatments and concentrations of free available chlorine[a] being used in washing.

Lot No.	Washing method	Count before washing	Count after washing with water containing free available chlorine in the concentrations: 0 ppm	10 ppm	20 ppm	100 ppm
60	12-dip treatment P (Q=1)	520,000	69,000		70,000	
61	12-dip treatment P (Q=1)	81,000	6,500	10,000	9,100	
62	Spray treatment KE=6.4; Q=49	39,000	520			600
63	Spray treatment KE=6.4; Q=49	120,000	2,900			1,200
64	Spray treatment KE=6.4; Q=49	230,000	2,800			13,000
65[b]	Flume treatment Q=0.5	100,000	8,200			9,100
66[c]	Flume treatment Q=0.5	66,000	3,800			5,000

[a]In each case in which free available chlorine was present in the water at the beginning of the operation, some chlorine in this form was found to remain after the operation.
[b]Effectiveness of flume method on lot 65 was 91.4%.
[c]Effectiveness of flume method on lot 66 was 93.3%.

Practical Operating Conditions for Washers

The lower range of Q values (Q values <15) for which data have been presented is important in regard to plant operations, since this involves practical conveyor belt speeds (e.g. Q values of 8.5 and 17 were achieved using belt speeds of 8 and 16 ft/min, respectively). To save wear and tear on equipment and to keep operating costs low, conveyor belts used for this class of equipment should not exceed a speed of 10 to 15 ft/min. The lower the speed the better. Con-

TABLE VII. Percentage washing effectiveness (as measured by a bacteriological method) obtained by passing haddock under an effective spray.

Oldest-caught haddock (>5 days caught-age)				Newest-caught haddock (<4 days caught-age)					
Initial count/cm²	Number of passes on conveyor belt under spray			Initial count/cm²	Number of passes on conveyor belt under spray				
	1	2	4		1	2	4	5	10
	(Q = <2)	(Q = <1)	(Q = <½)		(Q = <2)	(Q = <1)	(Q = <½)	(Q = <⅛)	(Q = <1/16)
1,000,000	96.8	98.7	99.6	758,000	96.9	96.2	99.7	–	–
2,000,000	96.6	99.3	99.3	400,000	96.2	–	–	99.8	99.8

TABLE VIII. Percentage washing effectiveness (as measured by a bacteriological method) obtained by washing flounders in a rotary fish machine.

Oldest-caught flounders (>5 days caught-age)			Newest-caught flounders (<5 days caught-age)		
Initial count/cm²	Washing time in rotary washer		Initial count/cm²	Washing time in rotary washer	
	1 min	4 min		1 min	4 min
	(Q≈2)	(Q≈½)		(Q≈2)	(Q≈½)
7,800,000	99.1	99.9	1,400,000	99.8	99.9

veyor belts travelling at speeds of 8 and 16 ft/min deliver approximately 150 and 300 lb/min, the fish being one layer deep with no overlapping of individuals. A belt travelling at the lower speed and loaded as described should supply about 20 cutters working on market cod. Fortuitously, this is also the range of Q values in which washing effectiveness under a water spray can be high (Fig. 2) and in which washing effectiveness seems to be independent of caught-age of the fish (Table IIIB, column H and I).

In these experiments, the kinetic energies of the water used to obtain high washing effectiveness at Q values of 8.5 to 17 were obtained using practical water pressures of 8 to 24 lb/sq inch gauge. Any pressure in the range of 8 to about 50 was found to be practicable with pressures of 20 lb/sq inch and above being most satisfactory for determining definite spray patterns from nozzles. This range will vary somewhat with the style, design features and size of nozzle. The designer should observe the points noted below in order to provide the required kinetic energy of water per unit of time uniformly over the area of the belt: (i) choice of water pressure, (ii) type and design of nozzles, (iii) arrangement of nozzles, and (iv) spacing of nozzles. In effect, this choice will determine the length of conveyor belt. Facilities should be provided on the belt for washing the fish from all sides and for hosing or otherwise rinsing the gut cavity. Water in addition to that already specified will have to be provided for washing the gut cavity and should be applied prior to spraying the skin.

The curves in Fig. 2 and 3 (based on the use of $\frac{1}{4}$U6520 nozzles) may be used to advantage in the following manner. If one is operating over a Q range of 10 to 15 and desires 98.5 to 99.0% washing effectiveness, work requirements may range from as low as 1 to about 4 (Fig. 2) corresponding to a pressure range of 5 to 16 lb/sq inch gauge (Fig. 3). Assuming that another curve, HC

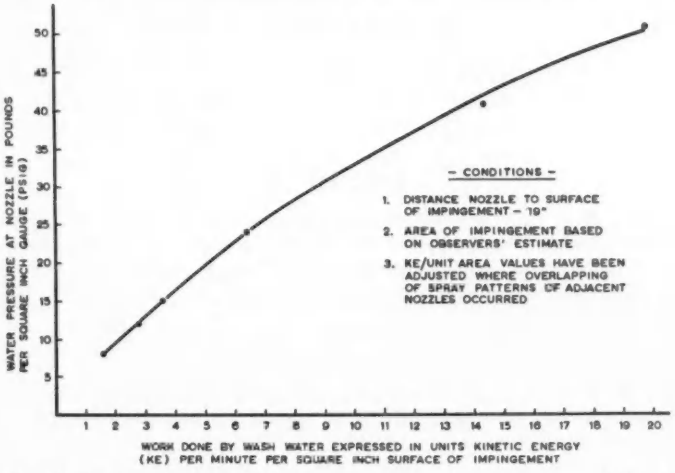

WATER PRESSURE AT NOZZLE IN POUNDS PER SQUARE INCH GAUGE (PSIG)
50
45
40
35
30
25
20
15
10
5
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
WORK DONE BY WASH WATER EXPRESSED IN UNITS KINETIC ENERGY (KE) PER MINUTE PER SQUARE INCH SURFACE OF IMPINGEMENT
– CONDITIONS –
1. DISTANCE NOZZLE TO SURFACE OF IMPINGEMENT – 19"
2. AREA OF IMPINGEMENT BASED ON OBSERVERS' ESTIMATE
3. KE/UNIT AREA VALUES HAVE BEEN ADJUSTED WHERE OVERLAPPING OF SPRAY PATTERNS OF ADJACENT NOZZLES OCCURRED

FIG. 3. Calculated correlation between water pressure at nozzle and kinetic energy exerted per min per sq inch of surface of impingement (conversion factors: 1 psi = 7.03×10^{-2} kg/cm^2; 1 ft-lb/min = 13.8×10^{-2} kg-m/min).

(Fig. 2) could be drawn for conditions of very high (99% to 99% +) spray washing effectiveness (only two points available), we could expect work requirements of about 7.5 to 12 in a Q range of 10 to 15, corresponding to a water pressure range of about 26 to 37 lb/sq inch gauge (Fig. 3). In selecting a Q value below 15 and preferably as near 10 as is practicable, the designer has to give appropriate recognition to the conveyor belt loading factor, also belt speed and arrangement of nozzles to ensure full coverage of the required area of belt at the desired water pressure.

CONCLUSIONS

1. Spraying is more efficient than fluming or dipping in removing bacteria from the exterior surfaces of fish in that it requires less water to achieve a given level of washing effectiveness.

2. Some form of flushing of the abdominal cavity is required to minimize bacterial contamination of cutting boards.

3. In spray washing, the amount of fish which can be washed to a chosen degree of effectiveness by a constant amount of water is increased when the kinetic energy of the water reaching the fish is increased.

4. A spray of given characteristics is less effective in washing fish if it is directed at the fish from below a steel mesh conveyor belt than if it is directed at the fish from above the belt.

5. For plant operations caught-age does not appear to have an effect on washing effectiveness when the fish are sprayed effectively.

6. Water pressures ranging from 8 to about 50 lb/sq inch were all found to produce high washing effectiveness under the spray method.

7. The presence of free available chlorine in wash water does not seem to increase the effectiveness of fish-washing operations.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the technical assistance of Helen Varga and Astrid M. Doucette of the Fish Inspection Laboratory, Halifax, and Rosalie (Triggs) Gillespie, Ottawa, who assisted in conducting bacterial assessment.

REFERENCES

CASTELL, C. H. 1947. The control of fillet contamination in fish plants: Part I—A survey of present conditions. *Prog. Rep. Atl. Coast Sta., Fish. Res. Bd. Canada*, No. 39, pp. 3–7.

1953. Reduction of bacterial contamination on fillets by washing the round fish and by the use of mechanical skinners. *Prog. Rep. Atl. Coast Sta., Fish. Res. Bd. Canada*, No. 56, pp. 10–14.

DYER, W. J., F. E. DYER AND M. SNOW. 1946. Amines in fish muscle. III. Spoilage of iced eviscerated cod. *J. Fish. Res. Bd. Canada*, 6: 403–413.

MULLAN, M. W., D. R. CONLEY AND M. D. BAXTER. MS, 1958. Bacteriological assessment of filleting operations. Presented at Department of Fisheries of Canada Inspection and Consumer Service, Annual Meeting, Ottawa.

TARR, H. L. A., AND A. W. LANTZ. 1949. The effect of mechanical washing of fish on the keeping quality of fillets prepared from them. *Prog. Rep. Pac. Coast Sta., Fish. Res. Bd. Canada*, No. 81, pp. 80–83.

Effect of Photoperiods on the Reactions of Juvenile Atlantic Salmon (*Salmo salar* L.) to Light Stimuli[1,2,3]

By A. T. Pinhorn[4] and C. W. Andrews

Memorial University of Newfoundland
St. John's, Nfld.

ABSTRACT

The reactions to light stimuli of juvenile Atlantic salmon exposed to photoperiods (light-exposed fish) and those exposed to control conditions (control fish) were compared. The light-exposed fish showed more activity and reacted more readily to stimuli than the control fish. Both the control and light-exposed fish exhibited a negative phototaxis at all light intensities except the very lowest where a slight positive phototaxis was obvious. The intensity of an intermittent light stimulus had very little effect on the intensity of the reaction in the light-exposed fish, while the control fish showed an increase in the intensity of the reaction with an increase in the intensity of the light stimulus. The control fish showed an increase in the reaction to the intermittent light stimulus the longer the stimulus was applied at the higher levels of stimulation, while the light-exposed fish showed this behavior at the lower levels of stimulation. The reactions to continuous light were similar to the reactions to intermittent light stimuli, but the light-exposed fish reacted more quickly to continuous light than the control fish. These differences in behavior are attributed to the increased activity and sensitivity of the light-exposed fish, resulting from their exposure to photoperiods.

INTRODUCTION

It has been demonstrated experimentally that the intensity and duration of light has an effect on the maturation processes of fish. Various species have been induced to spawn several months before their normal spawning season by exposing them to increasing amounts of daily light, decreasing amounts of daily light and continuous light, and this indicates an accelerated rate of maturation (Hoover, 1937; Hoover and Hubbard, 1937; Merriman and Schedl, 1941; Scrimshaw, 1944; Harrington, 1950, 1956; Kawamura and Otsuka, 1950; Hazard and Eddy, 1951; Medlen, 1951; Corson, 1955). However, upon exposing other species of fish to similar varying conditions of light, it was found that the spawning date was delayed, indicating a decelerated rate of maturation (Allison, 1951; Hazard and Eddy, 1951). From other experiments it was concluded that darkness or small amounts of light greatly depressed maturity and spawning in fish (Bullough, 1940; Rasquin, 1949; Rasquin and Rosenbloom, 1954). In a few cases light was found to have no effect on the maturation of fish (Burger, 1939; Matthews,

[1]Received for publication January 22, 1963.

[2]This paper is based on a section of a thesis submitted by the senior author in partial fulfilment of the requirements for the degree of Master of Science in Zoology at the Memorial University of Newfoundland.

[3]This investigation was supported by a grant from the National Research Council of Canada to Dr C. W. Andrews.

[4]Present address: Fisheries Research Board of Canada, Biological Station, St. John's, Nfld.

J. Fish. Res. Bd. Canada, **20**(5), 1963.
Printed in Canada.

1939; Merriman and Schedl, 1941), while in some species temperature seemed to be more important than light in this respect (Bullough, 1939; Burger, 1939). The discrepancies in the results of different workers probably resulted from the use of various species of fish which spawn at different seasons and under different conditions of natural light.

Since light has been found to affect spawning and maturity, it is conceivable that light could also be important at other stages in the development of fish. In the present study the effect of photoperiods on the change in behavior patterns of Atlantic salmon (*Salmo salar* L.) at the time of transformation from the parr to the smolt stage of development was investigated. Very little research has been done experimentally on the changes associated with this transformation in Atlantic salmon, but physically, the characteristic black markings of the parr give place to the silvery sheen of the smolts (Robertson, 1948; Hoar, 1958). Biochemically, the smolts are able to adapt to changes in the salinity of their environment much more readily than the parr and this ability is closely related to the thyroid gland (Rutter, 1904; Sumner, 1905; Scott, 1916; Hoar, 1939; Huntsman and Hoar, 1939; Fontaine, 1948, 1951; Hoar and Bell, 1950; Black, 1951). Regarding the behavior patterns, a detailed study has been done only on the Pacific salmon of the genus *Oncorhynchus*, where the behavior with respect to light stimuli, physical stimuli, water currents and light gradients is distinctly different in the parr and smolt stages of development (Hoar, 1951, 1952, 1953, 1954, 1955, 1956, 1958; Hoar *et al.*, 1952; Hoar *et al.*, 1957). Since Atlantic salmon are also of the family Salmonidae and indeed do undergo changes in physical appearance and biochemistry, it seems reasonable to assume that they undergo similar changes in behavior patterns at the time of parr–smolt transformation. Consequently, any effect of the photoperiods on the development and transformation of these juvenile salmon should result in differences in the behavior patterns of fish exposed to photoperiods and those exposed to control conditions. This was used as a working hypothesis in the present paper, in which the differences in their reactions to light stimuli are discussed.

MATERIALS AND METHODS

While the experiments were being performed the juvenile salmon were held in 6 wooden tanks through which water was continually circulated from a larger wooden reservoir tank. The temperature of the water was controlled by means of refrigeration plates located in the reservoir tank and connected to a refrigeration unit. The water was well aerated and mixed by means of compressed air bubbling from air stones located in each tank. Three fluorescent light bulbs above each tank, when turned on, gave a light intensity of 25 ft-c at the surface of the water. All light intensities were measured with an exposure photometer, Model 200 M (Photovolt Corporation, New York), which had a sensitivity of 0.02 ft-c.

The experiments were performed in the Biology Department of the Memorial University of Newfoundland during August 1959, December 1959, and January 1960. The fish were obtained from the Margaree Hatcheries, Frizzleton, Nova

Scotia, and were all in fry stage, having been hatched in the spring of 1958. They ranged in length from approximately 2–4 cm at the beginning of the experiments to 6–8 cm at the end of the experiments. The fish were fed on fresh beef liver twice daily at the lower acclimation temperatures and three times daily at the higher acclimation temperatures. The acclimation temperature was maintained at 15° C during the summer, 10° C during the autumn and 5° C during the winter. Two groups of fish were used, all initially of the same chronological age. One group, the light-exposed fish, was subjected to a light intensity of 25 ft-c for 16 hr each day and darkness for the remaining 8 hr. The second group, the control fish, was subjected to a light intensity of less than 1 ft-c for 16 hr per day and darkness for the remaining 8 hr. It is realized that these control fish were not subjected to light conditions identical to those found in nature but rather to reduced light. However, it is felt that they served as a suitable control group in these experiments.

The experiments testing the reactions of juvenile Atlantic salmon to intermittent light stimuli were divided into 2 groups, referred to as Series I and Series II. The methods of observation in each case were essentially the same but in the Series I experiments the size of the apparatus was much smaller than in the Series II experiments. Also, 5 fish were used at a time in the Series I experiments and the water temperature was maintained at 15° C, whereas in the Series II experiments 10 fish were used at a time and the water temperature decreased from 10° C to 5° C during the experimental period.

In the Series I experiments a glass aquarium (51 cm long, 30 cm wide and 29 cm deep) was used (Fig. 1). A centre board divided the aquarium into 2 equal compartments, while a space was left below the board so that the fish could swim freely from one compartment to the other. A light of desired intensity was located directly above the centre of each compartment and the centre board extended above the middle of the tank between the 2 light bulbs, so that each compartment could be illuminated independently of the other. The entire apparatus was surrounded by black curtains to ensure that very little external light entered the experimental tank. The light intensity at the surface of the water could be varied by adjusting the iris diaphragm interposed between the light source and the water surface, by varying the distance between the light bulb and the water surface and by using different wattages of light bulbs. Observation of the fish was made through a peekhole in the curtain.

The apparatus for the Series II experiments was similar to that described above (Fig. 2). However, the wooden tank was larger (244 cm long, 30 cm wide and 30 cm deep). In addition, a ground glass plate was interposed between the light source and the water surface and 3 or 4 light bulbs instead of 1 were used as a light source. The observations were made through a glass end in the tank. Water flowed continually in at one end and out at the other end of the tank, so that the temperature remained fairly constant throughout any experiment. The water current created by the water flowing into the tank was not sufficient to stimulate rheotaxis and in any case the fish were prevented from entering the current area by a screen placed at a distance from the end of the tank (Fig. 2).

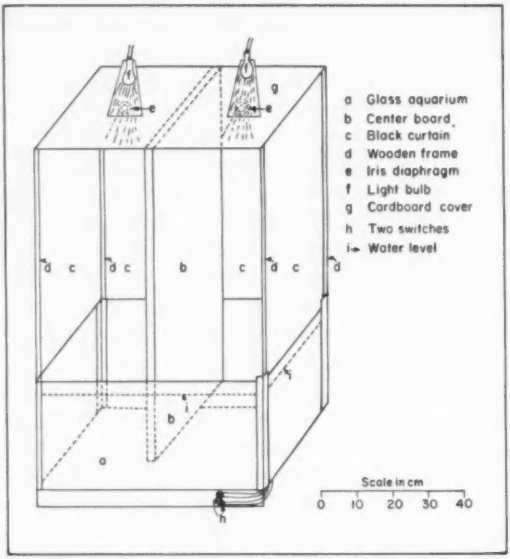


FIG. 1. Diagram of apparatus used in the study of the reactions of juvenile Atlantic salmon to light stimuli (Series I).

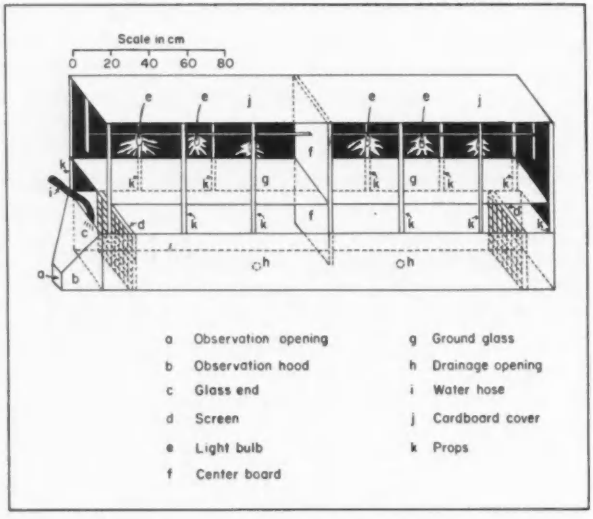


FIG. 2. Diagram of apparatus used in the study of the reactions of juvenile Atlantic salmon to light stimuli (Series II).

In the Series I experiments 5 fish were placed in the tank and left in complete darkness for 30 min. A light of desired intensity was then switched on over one compartment, so that this compartment was illuminated and the other was relatively dark. After 10 sec had passed, the number of fish in the illuminated compartment was counted. Another 20 sec were allowed to elapse and the number of fish in this compartment was again counted. Finally, another 30 sec were allowed to pass and another count of the number of fish was made, at 60 sec after the light was turned on. The lighting was then reversed, the light over the illuminated compartment being turned off and the one over the darkened compartment being turned on. The former illuminated compartment now became darkened and the darkened compartment became illuminated. The above procedure was then repeated for 60 sec. The lights were reversed in this way four times, giving a total of 5 counts of the number of fish in the illuminated compartment at each of 10 sec, 30 sec and 60 sec after the stimulus was applied. These periods after the stimulus was applied will hereafter be referred to as the 10-sec level, the 30-sec level and the 60-sec level, respectively. A different group of 5 fish was then placed in the tank and a duplicate experiment was performed with a procedure identical to that above. Ten of these experiments were performed at 0.1 ft-c and 0.2 ft-c, for both control and light-exposed fish, giving a total of 50 counts at each of the 10-, 30- and 60-sec levels, whereas at 2.0 ft-c and 200.0 ft-c, 5 experiments were performed giving a total of 25 counts at each of these levels. However, at 20.0 ft-c, 5 experiments were performed for control fish and 2 experiments for light-exposed fish, giving a total of 25 and 10 counts, respectively, at each of the 10-, 30- and 60-sec levels.

The observations in the Series II experiments were of 2 types. In one case the procedure was similar to that in the Series I experiments, but the fish were left in the light intensity being used for 60 min before subjected to darkness for 30 min. This was to ensure that the eyes of both the control and light-exposed fish would be in the same state of light adaptation at the beginning of the experiments. It was assumed that, since these 2 groups of fish were living under different light conditions in the holding tanks prior to the experiments, this might have some effect on their reactions to the light stimuli, because of different degrees of light or dark adaptation (Ali, 1959). At the end of the dark adaptation period the experiments were performed with a procedure identical to that used in the Series I experiments. Ten reversals of the lights were made in these experiments, giving a total of 10 counts at each of the 10-, 30- and 60-sec levels. The lights were then switched off and the same fish were left in the tank for 30 min. The experiment was then repeated. Ten of these experiments were performed on the same group of fish, giving a total of 100 counts at each of the 10-, 30- and 60-sec levels. A different group of 10 fish was then placed in the tank and 10 experiments were performed with a procedure identical to that above. When the duplicate experiments were combined, a total of 200 counts was made at each of the 10-, 30- and 60-sec levels. Experiments were performed at 20.0 and 200.0 ft-c.

The second type of observation tested the reactions of the fish to continuous light. Ten fish were again placed in the tank and left in the light for 60 min.

The light over one compartment was then turned off and the fish left for an additional 30 min. At the end of this time the number of fish in the illuminated compartment was counted at 30-sec intervals for 15 min, giving a total of 30 counts per experiment. The lights were then reversed and the fish left for 30 min under these conditions. A second experiment was then performed with a procedure identical to the first. Seven experiments were performed in this way on the same group of fish, giving a total of 210 observations. A duplicate group of experiments was then performed on 10 different fish with a procedure identical to the first group. This gave a total of 420 counts on 20 fish. Experiments were conducted at 20.0 and 200.0 ft-c.

In addition to the usual counts, observations were made on the reaction times of these fish to a light stimulus. In the procedure outlined above for the reaction to continuous light of 200.0 ft-c intensity, the fish were observed for 10 min immediately following the reversal of the lights and the time was recorded when each fish entered the shaded compartment. This gave some measure of the time taken for these fish to react to a light stimulus.

RESULTS

Andrews and Pinhorn (MS, 1962) have presented results which clearly indicate that exposing juvenile Atlantic salmon fry of approximately 7 cm in length to photoperiods results in the loss of parr marks and the onset of the smolt condition. General observations in the present study have corroborated these findings.

General Behavior of Fish

In the Series I experiments using the glass aquarium, it was found that the control fish reacted only slightly when lights of low intensity were used as stimuli. However, as the intensity of the stimulus was increased by the use of higher light intensities, the magnitude of the reaction increased until almost a total response occurred at the highest light intensity used (200.0 ft-c). The fish did not respond at all at the low light intensities, until 2 or 3 stimuli had been applied by flashing the light on over one compartment and off over the other at 1-min intervals. A fish was then seen to sway its body right and left and swim slowly into the opposite compartment or around the same compartment once or twice. At the highest light intensity the fish darted into the dark compartment immediately after the light was turned on and, as a rule, remained there. Occasionally, a fish would move from the dark to the light but only to dart back again after a little while.

The light-exposed fish in the Series I experiments behaved very differently from the control fish. Whereas the control fish remained very quiet except at high light intensities, and remained nearly always on the botton of the aquarium, the light-exposed fish were very active at all light intensities studied, moving freely from one compartment to the other with apparent disregard for the absolute light intensity to which they were subjected. In addition to the horizontal movements into and out of the light and dark compartments, these light-exposed

TABLE I. Tests of significance between the numbers of fish in the light and dark compartments at each light intensity. P-values marked with an asterisk

TABLE I. Tests of significance between the numbers of fish in the light and dark compartments at each light intensity. P-values marked with an asterisk are significant at the 0.05 level.

	0.1 ft-c			0.2 ft-c			2.0 ft-c		
	10 sec	30 sec	60 sec	10 sec	30 sec	60 sec	10 sec	30 sec	60 sec
Control fish									
t	0.4	2.4	1.3	0.6	0.8	2.2	1.2	2.3	3.1
P	0.70	0.02*	0.20	0.55	0.45	0.025*	0.25	0.02*	<0.01*
Light-exposed fish									
t	1.8	2.8	5.4	1.5	2.4	4.1	1.7	2.8	4.9
P	0.07	<0.01*	<0.001*	0.15	0.02*	<0.001*	0.07	<0.01*	<0.001*

	20.0 ft-c						200.0 ft-c					
	Series I			Series II			Series I			Series II		
	10 sec	30 sec	60 sec	10 sec	30 sec	60 sec	10 sec	30 sec	60 sec	10 sec	30 sec	60 sec
Control fish												
t	0.05	2.4	4.0	0.5	0.8	3.9	4.6	6.7	9.4	1.0	2.0	5.3
P	>0.90	0.02*	<0.001*	0.60	0.45	<0.001*	<0.001*	<0.001*	<0.001*	0.30	<0.05*	<0.001*
Light-exposed fish												
t	0.9	1.7	3.1	1.2	0.5	1.9	1.3	3.1	3.1	0.4	0.4	1.0
P	0.35	0.07	<0.01*	0.25	0.60	0.06	0.20	<0.01*	<0.01*	0.70	0.70	0.30

fish also made vertical movements from the bottom of the tank to the surface of the water, and some even ventured to jump over the top of the tank. The fish that rose to the surface usually remained quiet there for varying periods of time, orienting themselves at a 45 degree angle with the water surface.

In the Series II experiments the behavior of the control and light-exposed fish was similar to that in the Series I experiments. The main difference was the decreased activity of the fish in the Series II experiments. The fish were less reactive to stimuli of all kinds, both to movements on the part of the observer and to stimuli in the experiments. Less activity was exhibited by these fish in quiet water, but, relatively speaking, the light-exposed fish were still more active than the control fish. This lower level of activity was attributed to the lower acclimation temperature of the Series II experiments (10° C to 5° C).

Reactions to Light Stimuli, Series I Experiments

The fish used in the Series I experiments were acclimatized to a temperature of 15° C. The light-exposed fish were subjected to light of 25 ft-c intensity and 16 hr daily duration for 4240–5200 hr (265–325 days).

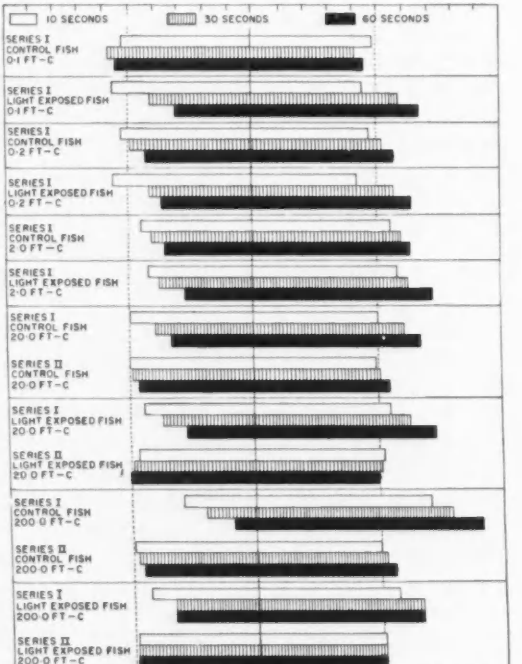

10 SECONDS
30 SECONDS
60 SECONDS
SERIES I CONTROL FISH 0·1 FT-C
SERIES I LIGHT EXPOSED FISH 0·1 FT-C
SERIES I CONTROL FISH 0·2 FT-C
SERIES I LIGHT EXPOSED FISH 0·2 FT-C
SERIES I CONTROL FISH 2·0 FT-C
SERIES I LIGHT EXPOSED FISH 2·0 FT-C
SERIES I CONTROL FISH 20·0 FT-C
SERIES II CONTROL FISH 20·0 FT-C
SERIES I LIGHT EXPOSED FISH 20·0 FT-C
SERIES II LIGHT EXPOSED FISH 20·0 FT-C
SERIES I CONTROL FISH 200·0 FT-C
SERIES II CONTROL FISH 200·0 FT-C
SERIES I LIGHT EXPOSED FISH 200·0 FT-C
SERIES II LIGHT EXPOSED FISH 200·0 FT-C
90 80 70 60 50 40 30 20 10 0 10 20 30 40 50 60 70 80 90 100
PERCENT OF FISH IN LIGHTED HALF OF TANK
PERCENT OF FISH IN DARKENED HALF OF TANK

Fig. 3. Reactions of juvenile Atlantic salmon to intermittent light stimuli. (See text for explanation of 10, 30 and 60 seconds and Series I and Series II.)

The variations in the reactions of the fish to the light stimuli were found to be fairly large. However, this is not surprising since in any behavior study the reactions are never of the all-or-none type but rather those reactions characterized by the species are prevalent over an observation period. The small size of the apparatus and the small number of fish used per experiment may have been contributing factors.

In the statistical analyses of the results, $P = 0.05$ was used as the level of significance.

CONTROL FISH. At a light intensity of 0.1 ft-c a *t*-test shows that the percentage of control fish in the light was significantly greater than that in the dark at the 30-sec level (Table I and Fig. 3). At 0.2 ft-c the percentage of fish in the light was significantly less than that in the dark at the 60-sec level, while at both 2.0 and 20.0 ft-c, the percentage of the fish in the light was significantly less at both the 30-sec level and the 60-sec level. At 200.0 ft-c the reaction was very marked with a significantly lesser percentage in the light at the 10-, 30- and 60-sec levels (Table I and Fig. 3).

There was very little difference among the percentages of fish in the light in the range of light intensities 0.1–20.0 ft-c (Fig. 3). A tendency toward a lesser percentage of fish in the light at the higher light intensities is apparent but is by no means pronounced. In comparing the percentages of fish at successive light intensities significant differences were found between 0.1 and 0.2 ft-c at the 30- and 60-sec levels but none were found between 0.2 and 2.0 ft-c or 2.0 and 20.0 ft-c (Table II). There seems to be a light-seeking tendency at 0.1 ft-c since when 0.1 ft-c was compared with 20.0 ft-c, significant differences were found at the 30- and 60-sec levels whereas when 0.2 ft-c was compared with 20.0 ft-c no significant differences were found. . Outside of this range the response is very different since the percentage of fish in the light for 200.0 ft-c is significantly less than that for 20.0 ft-c at the 10-, 30- and 60-sec levels (Table II).

In comparing the percentage of fish in the light at each of the 3 time levels after the light stimulus was applied, no significant difference was found at 0.1, 0.2, or 2.0 ft-c, whereas there was a significant difference for 20.0 ft-c, the percentage in the light at 60 sec being significantly less than at 10 sec (Table III and Fig. 3). At 200.0 ft-c the percentage in the light at 30 sec is not significantly different from the percentage at 10 sec, whereas the percentage at 60 sec is significantly less than that at either 10 or 30 sec.

Although the total numbers of movements of the control fish from the dark to the light, or vice versa, at each light intensity were not recorded, some measure of the change in the intensities of their reactions as the light intensity changed can be derived from a rather indirect treatment of the results. First, the number of fish in the light at 10 sec after the light was turned on is compared with the number at 30 sec after the light was turned on. Then the number in the light at 30 sec is compared with the number at 60 sec. These 2 comparisons are between counts in the first observation period. The number of fish in the dark compartment at the end of the first period is the number in the light compartment at the beginning of the second observation period. Therefore, by comparing the

TABLE II. Tests of significance between the numbers of fish in the light compartment at various light intensities. P-values marked with an asterisk are significant at the 0.05 level.

	Intensity compared	Control fish									Light-exposed fish								
		10 sec			30 sec			60 sec			10 sec			30 sec			60 sec		
		t	df	P	t	df	P	t	df	P	t	df	P	t	df	P	t	df	P
Series I	0.1 0.2	0.2	98	0.85	2.1	98	0.03*	2.2	98	0.03*	0.2	98	0.85	0.3	98	0.75	1.1	98	0.30
Series I	0.2 2.0	1.2	73	0.25	1.5	73	0.15	1.5	73	0.15	2.5	73	0.02*	0.9	73	0.35	1.7	73	0.10
Series I	2.0 20.0	0.8	48	0.40	0.1	48	0.98	0.7	48	0.50	0.2	33	0.90	0.04	33	>0.99	0.0	33	∞
Series I	20.0 200.0	3.1	48	<0.01*	3.1	48	<0.01*	4.5	48	<0.001*	0.0	33	∞	0.2	33	0.85	1.1	33	0.30
Series II	20.0 200.0	0.2	598	0.85	0.3	598	0.75	0.05	598	>0.90	0.5	598	0.60	0.4	598	0.70	1.3	598	0.20
Series I	0.1 20.0	0.3	73	0.75	3.1	73	<0.01*	3.6	73	<0.001*									
Series I	0.2 20.0	0.4	73	0.70	1.5	73	0.15	1.9	73	0.06									

TABLE III. Tests of significance between the numbers of fish in the light compartment at the 3 time levels for each light intensity. P-values marked with an asterisk are signficant at the 0.05 level.

	0.1 ft-c			0.2 ft-c			2.0 ft-c			20.0 ft-c						200.0 ft-c					
										Series I			Series II			Series I			Series II		
	t	df	P	t	df	P	t	df	P	t	df	P	t	df	P	t	df	P	t	df	P
Control fish																					
10 sec 30 sec	1.4	98	0.15	0.9	98	0.35	0.9	48	0.35	1.6	48	0.10	0.7	398	0.50	1.6	48	0.10	1.7	798	0.10
30 sec 60 sec	0.7	98	0.45	0.9	98	0.35	0.8	48	0.40	1.1	48	0.30	1.4	398	0.15	2.6	48	0.01*	1.8	798	0.07
10 sec 60 sec	0.6	98	0.55	1.7	98	0.10	1.7	48	0.10	2.6	48	0.01*	2.1	398	0.03*	4.4	48	<0.001*	3.5	798	<0.001*
Light-exposed fish																					
10 sec 30 sec	2.8	98	<0.01*	3.0	98	<0.01*	0.8	48	0.40	0.5	18	0.60	0.7	398	0.45	1.2	48	0.25	0.05	798	>0.90
30 sec 60 sec	1.8	98	0.07	1.3	98	0.20	1.5	48	0.15	1.0	18	0.30	0.6	398	0.50	0.0	48	∞	0.3	798	0.75
10 sec 60 sec	4.8	98	<0.001*	4.2	98	<0.001*	2.3	48	0.02*	1.7	18	0.10	1.3	398	0.20	1.1	48	0.30	0.3	798	0.75

number in the light at 10 sec after the lights were reversed in the second observation period with the number in the dark at the end of the first observation period, a measure of the net reactions in the first 10 sec is possible. By repeating this procedure for each observation period in each experiment, summing the total numbers of reactions for all the experiments and dividing this total by the number of counts, an average number of reactions can be obtained for the first 10 sec, the first 30 sec and the total 60 sec after the light was turned on.

In the analyses of the reactions it seemed best to separate them into positive reactions (movements toward the light), negative reactions (movements away from the light) and zero reactions (no movements with respect to the light). The percentages of positive, negative and zero reactions for the total 60-sec period at each light intensity are plotted in Fig. 4.

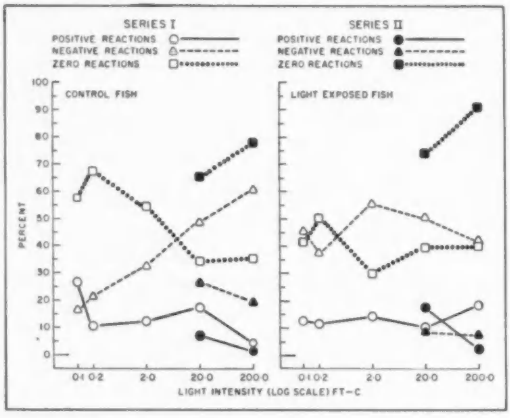


FIG. 4. Variations in the percentages of positive, negative and zero reactions of juvenile Atlantic salmon to intermittent light stimuli.

The positive reactions remained fairly constant throughout the whole range of light intensities studied (0.1–200.0 ft-c), although there is a marked decrease between 0.1 and 0.2 ft-c. The percentage of negative reactions increased steadily between 0.1 and 200.0 ft-c. To offset this increase, the percentage of zero reactions decreased over the same range of intensities.

LIGHT-EXPOSED FISH. At both 0.1 and 0.2 ft-c there was a greater percentage of light-exposed fish in the light compartment at the 10-sec level and this may be a light-seeking tendency (Fig. 3). However, there was a negative response to the light at these intensities with a significantly lesser percentage of fish in the light at both the 30- and 60-sec levels (Table I). At 2.0 ft-c there was a significant negative response at the 30- and 60-sec levels, while at 20.0 ft-c there was a significant negative response at the 60-sec level only. This apparent anomaly is probably because of the small numbers of counts (10) made at 20.0 ft-c. The response at 200.0 ft-c was negative at both the 30- and 60-sec levels, although

the light-exposed fish did not respond nearly as strongly as the control fish to this light intensity (Table I).

In the range of light intensities 0.1–200.0 ft-c there was only one significant difference in the percentage of fish in the light compartment (between 0.2 and 2.0 ft-c at the 10-sec level) when successive light intensities were compared or when the lowest was compared with the highest intensity (Table II), although a tendency to move into the dark at high intensities was evident (Fig. 3). The increase in response is not nearly as clear-cut as in the control fish, so that the light-exposed fish can be said to show no difference in the intensity of their response in this range of light intensities.

In comparing the responses at the 3 time levels, there was a significant decrease in the percentage of fish in the light between the 10- and 30-sec levels at 0.1 and 0.2 ft-c, but none between the 30- and 60-sec levels (Table III and Fig. 3). The decrease is also significant between the 10- and 60-sec levels. At 2.0 ft-c there was a significant difference in the response between the 10- and 60-sec levels only. Since there is a significant negative response at this light intensity, this would indicate that most of the reaction occurred within the first 10 sec.

The positive, negative and zero reactions of these light-exposed fish remained almost constant throughout the whole range of intensities studied, but the positive reactions were very few while the negative and zero reactions were more numerous (Fig. 4).

COMPARISON OF THE REACTIONS OF CONTROL AND LIGHT-EXPOSED FISH. At 0.1 ft-c there was a significantly greater percentage of control fish in the light at the 30- and 60-sec levels, thus indicating that the light-exposed fish reacted more strongly to this light intensity than the control fish (Table IV and Fig. 3). At 0.2, 2.0 and 20.0 ft-c, there was no significant difference in the percentage of control and light-exposed fish in the light, whereas at 200.0 ft-c the percentage of control fish in the light was significantly less than that of the light-exposed fish at the 10-, 30- and 60-sec levels.

REACTIONS TO LIGHT STIMULI, SERIES II EXPERIMENTS

The fish used in the Series II experiments were acclimatized to a temperature of 10° C to 5° C. The light-exposed fish were subjected to light of 25 ft-c intensity and 16 hr daily duration for 2176–4000 hr (136–250 days).

The variations in the responses of the individual groups of fish were smaller per number of fish than in the Series I experiments, probably because of the larger apparatus and lower temperature of the Series II experiments.

CONTROL FISH. The statistical analyses show that there was a significantly lesser percentage of fish in the light compartment at the 60-sec level for 20.0 ft-c and at the 30- and 60-sec levels for 200.0 ft-c (Table I and Fig. 3).

When the percentage of fish in the light at 20.0 ft-c was compared with the percentage at 200.0 ft-c, no significant difference was found at any of the 10-, 30- and 60-sec levels (Table II and Fig. 3). This is in contrast to the result found in the Series I experiments and may be atrributed to (a) the larger size of the tank in the Series II experiments, allowing more "living room" and less

TABLE IV. Tests of significance between the numbers of control and light-exposed fish in the light compartment at each light intensity. P-values marked with an asterisk are significant at the 0.05 level.

	0.1 ft-c			0.2 ft-c			2.0 ft-c			20.0 ft-c						200.0 ft-c					
										Series I			Series II			Series I			Series II		
	10 sec	30 sec	60 sec	10 sec	30 sec	60 sec	10 sec	30 sec	60 sec	10 sec	30 sec	60 sec	10 sec	30 sec	60 sec	10 sec	30 sec	60 sec	10 sec	30 sec	60 sec
t	0.9	3.3	4.6	0.6	1.2	1.3	0.4	0.4	1.4	0.6	0.1	0.6	0.7	0.6	2.6	2.1	2.7	5.0	0.7	0.8	2.2
df	98	98	98	98	98	98	48	48	48	33	33	33	398	398	398	48	48	48	798	798	798
P	0.35	0.001*	<0.001*	0.55	0.25	0.20	0.70	0.70	0.15	0.55	>0.90	0.55	0.45	0.55	0.01*	<0.05*	<0.01*	<0.001*	0.45	0.40	0.03*

crowding of fish, (b) the darker interior (black) of the tank in the Series II experiments giving a lower total light intensity with a given incident light intensity, (c) the lower temperature of the Series II experiments and (d) the ground glass plate causing a more diffuse illumination.

There was no significant difference in the percentage of fish in the light between the 10- and 30-sec levels, or the 30- and 60-sec levels at either 20.0 or 200.0 ft-c (Table III and Fig. 3). However, at both 20.0 and 200.0 ft-c the percentage of fish in the light was significantly less at 60 sec than at 10 sec.

The positive reactions of these control fish decreased, the negative reactions decreased and the zero reactions increased between 20.0 and 200.0 ft-c (Fig. 3). These results are in contrast to those found in the Series I experiments and are explained by the fact that the temperature dropped during the course of the experiments so that the 200.0 ft-c experiments were performed at a lower temperature than those at 20.0 ft-c. This lower temperature at 200.0 ft-c would result in a lesser number of movements and more zero reactions.

LIGHT-EXPOSED FISH. In general, the behavior of the light-exposed fish at the 2 light intensities was similar to that of the control fish. However, there was no significant difference in the percentage of fish in the light and dark compartments at either 20.0 or 200.0 ft-c (Table I and Fig. 3). This is in contrast to the results found in the Series I experiments for the light-exposed fish and may again be attributed to the larger size of the apparatus, the lower temperature, and the lower light intensity in the Series II experiments.

In comparing the percentage of fish in the light at 20.0 ft-c with the percentage at 200.0 ft-c, no significant difference was found (Table II and Fig. 3).

No significant difference was found in the percentage of fish in the light at any of the 10-, 30- and 60-sec levels for either of the light intensities (Table III and Fig. 3).

The positive reactions decreased between 20.0 and 200.0 ft-c, the negative reactions decreased and the zero reactions increased. These results are the same as those found for control fish in this series and are also attributed to temperature effects.

COMPARISON OF THE REACTIONS OF CONTROL AND LIGHT-EXPOSED FISH. At both 20.0 and 200.0 ft-c there was a significantly greater percentage of light-exposed fish in the light at the 60-sec level (Table IV and Fig. 3). This is the same result as was found in the Series I experiments.

REACTIONS TO CONTINUOUS LIGHT. The variations in these experiments were not too large, considering the greater number of fish used and the larger numbers of observations made.

A significantly lesser percentage of control fish was found in the light than the dark compartment at both 20.0 ft-c ($P<0.001$) and 200.0 ft-c ($P<0.001$) when these fish were subjected to continuous light (Fig. 5). In addition, the fish showed a significantly lesser percentage in the light at 200.0 ft-c than at 20.0 ft-c ($P<0.001$).

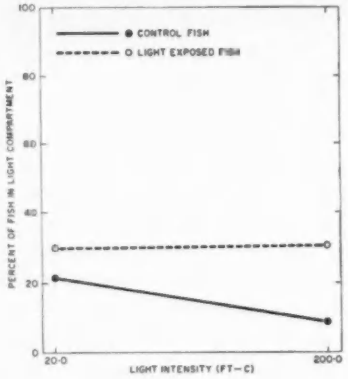


FIG. 5. Reactions of juvenile Atlantic salmon to continuous light.

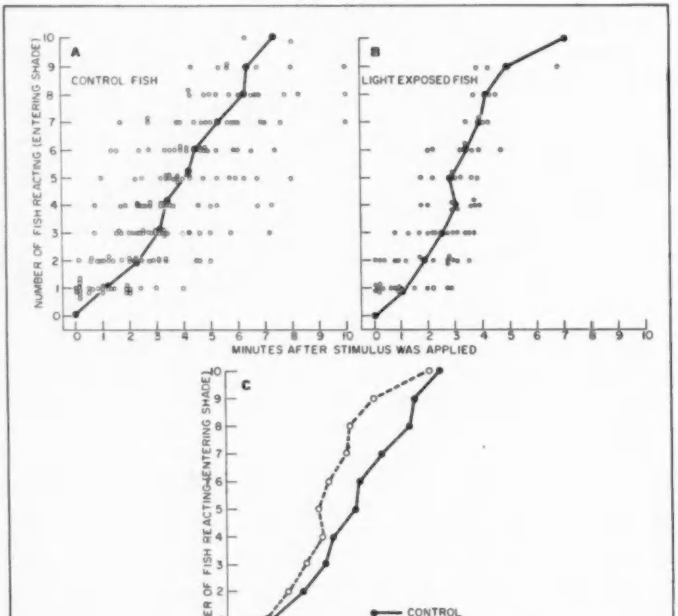


FIG. 6. Reaction times of juvenile Atlantic salmon to a light stimulus. (The stimulus was a light of 200.0 ft-c intensity flashed on fish previously kept in the shade.)

As was found for control fish, the light-exposed fish showed a significantly lesser percentage of fish in the light than the dark compartment at both 20.0 ft-c ($P<0.001$) and 200.0 ft-c ($P<0.001$) (Fig. 5). However, the intensity of the reaction of the light-exposed fish seemed to be unaffected by the intensity of light in this range, since there was no significant difference in the percentage of fish in the light at 20.0 and 200.0 ft-c.

There was a greater percentage of light-exposed than control fish in the light at both 20.0 ft-c ($P<0.001$) and 200.0 ft-c ($P<0.001$) (Fig. 5).

COMPARISON OF THE REACTION TIMES OF CONTROL AND LIGHT-EXPOSED FISH TO A LIGHT STIMULUS. Although there is a considerable spread in the points in Fig. 6, a trend toward a greater number of fish in the shade with increasing time after the stimulus was applied is apparent. The stimulus was a light of 200.0 ft-c intensity switched on fish previously kept in the shade. A comparison between the control and light-exposed fish (Fig. 6) indicates that the response of the light-exposed fish is more rapid than that of the control fish and at any given time a greater number of light-exposed fish have entered the shade.

DISCUSSION AND CONCLUSIONS

General Behavior

Evidence presented in this investigation has shown that the Atlantic salmon fry which were exposed to photoperiods were generally more active and reacted more readily to stimuli than the fish subjected to control conditions. Since it has been established that exposure to light is effective in accelerating the rate of development and maturity of widely different species of fish, and since Hoar (1951) showed that Pacific salmon of the genus *Oncorhynchus* exhibited more activity and a lower threshold of stimulation in the smolt stage than the parr stage, this difference in the behavior of control and light-exposed fish must have been a result of their exposure to different light conditions. It is believed that the light-exposed fish were physiologically more advanced and nearer the smolt stage of development than the control fish.

Reactions to Light Stimuli

It has been shown in the present study that both control and light-exposed fish showed a negative response to a flashing light stimulus (Fig. 3) and continuous light (Fig. 5). This was evident at all light intensities except the very lowest. This is at variance with the behavior of young Atlantic salmon in the natural habitat since they are frequently found in exposed, sunlit parts of rivers in daylight (Keenleyside, 1962). However, Neave (1955) found that the field observations for chum and pink fry were also at variance with laboratory observations by Hoar (1956), and this was because the laboratory fish acted as schools rather than individuals. In this connection Hoar *et al.* (1957) found that coho fry, coho smolts, sockeye fry and sockeye smolts were also photonegative under a light suddenly flashed on them or under continuous illumination. This is in agreement with the results found in this study for control and light-exposed fish. The coho and sockeye are the 2 species of Pacific salmon most closely related ecologically to the Atlantic salmon.

Control fish showed a stronger cover reaction (negative phototaxis) at higher than at lower light intensities, whereas the intensity of the reaction of the light-exposed fish was less affected by the light intensity, although the tendency toward increased response at high light intensity was still present (Fig. 3). This difference was believed to have resulted from the increased activity of the light-exposed fish, causing more random wandering from one compartment to the other. This tended to produce a greater number of light-exposed fish in the light compartment than would be warranted by the light intensity alone.

From a similar study, Hoar *et al.* (1957) showed that chum and pink fry were photopositive under light intensities ranging from 10 to 150 ft-c. However, coho fry tended to emerge under 10 and 45 ft-c and to retreat under 80, 115 and 150 ft-c, whereas coho smolts showed a uniform negative response under all light intensities. The results for sockeye fry and sockeye smolts were much more variable because of their increased activity but both types of fish were generally photonegative.

These results for coho fry agree fairly well with the results found for control fish, whereas the results for coho smolts agree with the results found for light-exposed fish in this study. The results for sockeye fry and sockeye smolts do not agree as well but complete agreement should not be expected, since these Pacific salmon are not of the same genus as the Atlantic salmon and even interspecific differences were found in the reactions of Pacific salmon to light. Also, the nature of the apparatus and the observations were somewhat different in the two studies. The fact that the light-exposed fish were living under conditions of light different from the control fish in the present study may have had some indirect effect on their behavior, through its effect on the retina or some other structure of the eye, but this aspect was not investigated further. In any event the difference in the bahavior of the control and light-exposed fish must have been a result of the exposure to light, since apart from light they were subjected to the same conditions in the holding tanks and the same conditions and stimuli in the experimental apparatus.

The control fish showed an increase in the number of fish in the shade, with increase in time after the light was turned on, only at the higher light intensities. The light-exposed fish, however, showed this behavior only at the lower light intensities (Fig. 3). This difference can be explained by several factors. At the higher light intensities the greater sensitivity of the light-exposed fish caused the major part of the negative reaction to occur within the first 10 sec after the light was turned on. Thus, there was no significant increase in the reaction after the first 10 sec. This greater sensitivity of the light-exposed fish caused their negative reaction to commence more quickly at the lower light intensities than in the control fish, whereas the sluggishness of reacting would tend to spread their reaction over a longer period of time. This would give the observed increase in the number of fish in the dark with increase in time. At the lower light intensities the control fish were so sluggish in their reaction that the increase in numbers in the dark compartment with increase in time did not show statistically, although the trend was still present.

Hoar *et al.* (1957) state that, at all light intensities, sockeye smolts exhibit a stronger negative reaction to the light than the corresponding fry, and the same was found to be true for the coho smolts and coho fry. However, they noted that the smolts of both species frequently swim into the most intense illuminations, because of their increased activity. It was found in the present study that at the lower intensities (0.1 ft-c) of light, the light-exposed fish showed a stronger negative reaction than the control fish, whereas at the highest light intensity (200.0 ft-c) the control fish showed a stronger negative reaction to the light. At 0.2, 2.0 and 20.0 ft-c there was no significant difference in the reaction of control or light-exposed fish. The fact that these results for control and light-exposed fish are in conflict with some of the literature results for fry and smolts seems to refute the hypothesis that the light-exposed fish are nearer the smolt stage than the control fish. However, the difference in the species of fish, the exposure to light and especially the increased activity of the light-exposed fish may have had some effect in masking their reactions.

The greater sensitivity of the light-exposed fish to the continuous light (Fig. 6) is in line with their greater general sensitivity to stimuli and their greater activity, and is believed to be because of a direct effect of the photoperiods on their rate of development.

In one of the observation periods with the intermittent light stimuli (Series II), there was a significantly greater number of light-exposed fish than controls in the lighted area of the tank, but this was attributed to these fish not having been fed during the experiments; they therefore sought the lighted areas more than usual. This is based on observations by Woodhead (1956) that hungry minnows (*Phoxinus phoxinus*) spent more time in the lighted areas when searching for food than in the darker areas.

Subjecting the fish to continuous light resulted in a greater negative reaction being exhibited by the control fish. This is the same result as was found generally with the intermittent light stimulus and is attributed to the greater activity of the light-exposed fish. It was noted that these fish were much more active in these particular experiments than the control fish. Whereas the light-exposed fish were frequently found to be on the move from one compartment to the other, the control fish were found to move into the dark compartment within the first 10 min after the light was turned on and to remain there, with only occasional fish moving into the light. The fact that the light was acting for a longer period of time in these experiments also allowed this difference in the behavior of the fish to show itself.

The lower temperature in the Series II experiments with the intermittent light stimulus was a factor responsible for the difference in the intensity of the reaction of the fish from that of the Series I experiments. Evidence in support of this statement is obtained from a comparison of their reactions under an intermittent light stimulus and continuous light (Series II). When using the intermittent stimulus in the Series II experiments, the fish showed a less intense reaction to the light than in the Series I experiments, whereas using continuous light there was a very significant reaction. With the intermittent stimulus the

fish had been adapted to darkness previous to the experiment and the low temperature together with the fact that the fish were subjected to the stimulus for only 60 sec resulted in very little reaction on their part. That is to say, the fish did not have time to react under the given conditions at such a low temperature (4–5° C). However, with the continuous light, the "stimulus" was applied for a period (30 min) long enough for the reaction to occur, even at the low temperature.

The general conclusion is that the exposure to photoperiods caused the fish to become more active under the conditions of the experiments and more sensitive to stimuli of all kinds. This caused reaction of the light-exposed fish to a flashing light stimulus of short duration to be significantly altered so that their negative reaction was less intense and less affected by the absolute light intensity than that of the control fish. Similarly the behavior of the 2 types of fish under continuous light was very different, with the controls again showing the greater negative reaction. It was shown that temperature could modify these reactions.

It is not possible on the basis of these experiments alone to comment on the significance of the reactions of these juvenile salmon to light. However, in a later paper in which various other behavior patterns will be described, their relationship to the natural habitat and the downstream migration will be discussed.

SUMMARY

1. Generally, the light-exposed fish were more reactive to stimuli of all kinds and showed more activity than the control fish.
2. Both the control and light-exposed fish were negatively phototactic to intermittent light stimuli at all light intensities studied except the very lowest.
3. In the Series I experiments the control fish showed very little difference in the intensity of their reactions to intermittent light stimuli in the range 0.1–20.0 ft-c. At 200.0 ft-c there was a marked difference in their response. The light-exposed fish showed no difference in their reactions among any of the light intensities studied. However, a trend toward a more intense negative reaction at successively higher light intensities was apparent for both control and light-exposed fish over the whole range of intensities studied (0.1–200.0 ft-c). In the Series II experiments no difference in the reactions was found between 20.0 and 200.0 ft-c for either control or light-exposed fish.
4. The control fish showed a significant increase in negative response the longer the stimulus was applied at the higher light intensities, whereas the light-exposed fish showed this behavior at the lower light intensities.
5. The control fish showed an increase in the percentage of negative reactions to the intermittent light stimuli, a decrease in the percentage of zero reactions and no change in the percentage of positive reactions, with increasing light intensity. The light-exposed fish showed no change in the percentage of negative, zero and positive reactions with increasing light intensity. Temperature modified these relationships to some extent in the Series II experiments.

6. The control fish showed a greater negative reaction to intermittent light stimuli than the light-exposed fish at the higher intensities whereas the light-exposed fish showed a greater negative reaction at the lower intensities.
7. Both control and light-exposed fish showed a significantly greater percentage in the dark at 20.0 and 200.0 ft-c, after they had been subjected to continuous light for 30 min. At both light intensities there was a greater percentage of light-exposed fish than control fish in the light. There was a significantly greater percentage of control fish in the light at 20.0 ft-c than at 200.0 ft-c, whereas the light-exposed fish showed no difference between the percentages in the light when 20.0 ft-c was compared with 200.0 ft-c.
8. The light-exposed fish reacted more rapidly to a light stimulus than the control fish.

ACKNOWLEDGMENTS

The authors are indebted to Dr W. Templeman, Mr A. M. Fleming and Mr A. W. May for the critical reading of the manuscript and to Mr H. R. Mullett for the drafting and Mr E. L. Rowe for the photography.

REFERENCES

ALI, M. A. 1959. The ocular structure, retinomotor and photobehavioral responses of juvenile Pacific salmon. *Canadian J. Zool.*, **37**: 965–996.

ALLISON, L. N. 1951. Delay of spawning in eastern brook trout by means of artificially prolonged light intervals. *Prog. Fish-Culturist*, **13**(3), pp. 111–116.

ANDREWS, C. W., AND A. T. PINHORN. MS, 1962. Effect of photoperiods on the onset of the smolt condition in juvenile Atlantic salmon (*Salmo salar* L.). [In preparation.]

BLACK, V. S. 1951. Changes in body chloride, density and water content of chum (*Oncorhynchus keta*) and coho (*O. kisutch*) salmon fry when transferred from fresh water to sea water. *J. Fish. Res. Bd. Canada*, **8**(3): 164–177.

BULLOUGH, W. S. 1939. A study of the reproductive cycle of the minnow in relation to the environment. *Proc. Zool. Soc. London*, **109**(8): 79–102.

1940. The effect of the reduction of light in spring on the breeding season of the minnow (*Phoxinus laevis* Linn.). *Ibid.*, **110**(10): 149–157.

BURGER, J. W. 1939. Some experiments on the relation of the external environment to the spermatogenetic cycle of *Fundulus heteroclitus* (L.). *Biol. Bull.*, **77**: 96–103.

CORSON, B. W. 1955. Four years' progress in the use of artifically controlled light to induce early spawning of brook trout. *Prog. Fish-Culturist*, **17**(3), pp. 99–102.

FONTAINE, M. 1948. Du rôle joué par les facteurs internes dans certaines migrations de poissons: Etude critique de diverses méthodes d'investigation. *J. Cons. Expl. Mer*, **15**(3): 284–294.

1951. Facteurs externes et internes régissant les migrations des poissons. *Année biol.*, **27**: 569.

HARRINGTON, R. W. 1950. Preseasonal breeding by the bridled shiner, *Notropis bifrenatus*, induced under light-temperature control. *Copeia* for 1950, No. 4, pp. 304–311.

1956. An experiment on the effects of contrasting daily photoperiods on gametogenesis and reproduction in the centrarchid fish, *Enneacanthus obesus* (Girard). *J. Exp. Zool.*, **131**: 203–223.

HAZARD, T. P., AND R. E. EDDY. 1951. Modification of the sexual cycle in brook trout (*Salvelinus fontinalis*) by control of light. *Trans. Am. Fish. Soc.*, **80**: 158–162.

HOAR, W. S. 1939. The thyroid gland of the Atlantic salmon. *J. Morphol.*, **65**: 257–296.

1951. The behaviour of chum, pink and coho salmon in relation to their seaward migration. *J. Fish. Res. Bd. Canada*, **8**(4): 241–263.

1952. Thyroid function in some anadromous and landlocked teleosts. *Trans. Roy. Soc. Canada*, Ser. 3, Sect. V, **46**: pp. 39–53.

1953. Control and timing of fish migration. *Biol. Rev.*, **28**: 437–452.

1954. The behaviour of juvenile Pacific salmon, with particular reference to the sockeye (*Oncorhynchus nerka*). *J. Fish. Res. Bd. Canada*, **11**(1): 69–97.

1955. Phototactic and pigmentary responses of sockeye salmon smolts following injury to the pineal organ. *Ibid.*, **12**(1): 178–185.

1956. The behaviour of migrating pink and chum salmon fry. *Ibid.*, **13**(3): 309–325.

1958. The evolution of migratory behavior among juvenile salmon of the genus *Oncorhynchus*. *Ibid.*, **15**(3): 391–428.

HOAR, W. S., AND G. M. BELL. 1950. The thyroid gland in relation to the seaward migration of Pacific salmon. *Canadian J. Zool.*, **28**: 126–136.

HOAR, W. S., M. H. A. KEENLEYSIDE AND R. G. GOODALL. 1957. Reactions of juvenile Pacific salmon to light. *J. Fish. Res. Bd. Canada*, **14**(6): 815–830.

HOAR, W. S., D. MACKINNON AND A. REDLICH. 1952. Effects of some hormones on the behavior of salmon fry. *Canadian J. Zool.*, **30**: 273–286.

HOOVER, E. E. 1937. Experimental modification of the sexual cycle in trout by control of light. *Science*, **86**: 425–426.

HOOVER, E. E., AND H. E. HUBBARD. 1937. Modification of the sexual cycle in trout by control of light. *Copeia* for 1937, No. 4, pp. 206–210.

HUNTSMAN, A. G., AND W. S. HOAR. 1939. Resistance of Atlantic salmon to sea water. *J. Fish. Res. Bd. Canada*, **4**(5): 409–411.

KAWAMURA, T., AND S. OTSUKA. 1950. On acceleration of the ovulation in the goldfish. [In Japanese with an English summary.] *Japanese J. Ichthy.*, **1**(3): 157–165.

KEENLEYSIDE, M. H. A. 1962. Skin-diving observations of Atlantic salmon and brook trout in the Miramichi River, New Brunswick. *J. Fish. Res. Bd. Canada*, **19**: 625–634.

MATTHEWS, S. A. 1939. The effects of light and temperature on the male sexual cycle in *Fundulus heteroclitus*. *Biol. Bull.*, **77**: 92–95.

MEDLEN, A. B. 1951. Preliminary observations on the effects of temperature and light upon reproductions in *Gambusia affinis*. *Copeia* for 1951, No. 2, pp. 148–152.

MERRIMAN, D., AND H. P. SCHEDL. 1941. The effects of light and temperature on gametogenesis in the four-spined stickleback, *Apeltes quadracus* (Mitchill). *J. Exp. Zool.*, **88**: 413–449.

NEAVE, F. 1955. Notes on the seaward migration of pink and chum salmon fry. *J. Fish. Res. Bd. Canada*, **12**: 369–374.

RASQUIN, P. 1949. The influence of light and darkness on thyroid and pituitary activity of the characin, *Astyanax mexicanus*, and its cave derivatives. *Bull. Amer. Mus. Nat. Hist.*, **93**: 497–532.

RASQUIN, P., AND L. ROSENBLOOM. 1954. Endocrine imbalance and tissue hyperplasia in teleosts maintained in darkness. *Bull. Amer. Mus. Nat. Hist.*, **104**: 359–426.

ROBERTSON, O. H. 1948. The occurrence of increased activity of the thyroid gland in rainbow trout at the time of transformation from parr to silvery smolt. *Physiol. Zool.*, **21**: 282–295.

RUTTER, C. 1904. Natural history of the Quinnat salmon. *Bull. U.S. Fish Comm.* for 1902, **22**: 65–141.

SCOTT, G. G. 1916. The evolutionary significance of the osmotic pressure of the blood. *Amer. Nat.*, **59**: 663–691.

SCRIMSHAW, N. S. 1944. Superfetation in poeciliid fishes. *Copeia* for 1944, No. 3, pp. 180–183.

SUMNER, F. B. 1905. The physiological effects upon fishes of changes in density and salinity of water. *Bull. U.S. Bur. Fish.*, **25**: 53–108.

WOODHEAD, P. M. J. 1956. The behaviour of minnows (*Phoxinus phoxinus* L.) in a light gradient. *J. Exp. Biol.*, **33**: 257–270.

Pollock (*Pollachius virens* (L.)) in the Bay of Fundy[1]

By D. H. Steele[2]

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

Observations made on the biology of the pollock in the western Atlantic, and primarily in the Bay of Fundy region of the northern Gulf of Maine, are presented. The largest landings of pollock in the western Atlantic are made in this area (ICNAF Division 4X). The best catches of large fish are made at temperatures above 1.1°C, at depths of 20–100 fathoms (35–185 m) on the edges of shoals and banks where food is abundant. Spawning occurs in the winter and takes place in the southern Gulf of Maine and probably also on the Scotian Shelf, but not in the northern Gulf of Maine. The Bay of Fundy pollock are recruited from spawning in the southern Gulf of Maine and possibly on the Scotian Shelf. The pollock found in the Bay of Fundy appear to remain separate from those of the southern Gulf of Maine and the Scotian Shelf in the summer, but migrate south, spawn and probably mix with those of the southern Gulf of Maine, and possibly also those of the Scotian Shelf in the winter. The offshore pollock have a regular gradient in size across the Bay of Fundy; large fish (65–85 cm) are caught on the New Brunswick side, medium-sized fish (60–75 cm) around Grand Manan and smaller fish (45–60 cm) off western Nova Scotia. Catches with different size compositions are also found in small areas. Segregation by size into schools is therefore an important feature of pollock behaviour. The growth rate of pollock is rapid until the approximate time of sexual maturity, which occurs at ages of 4–7 years (50–65 cm) in the males and 5–7 years (55–70 cm) in the females. The growth rate of the immature and young, mature fish is similar to that recorded for other areas, but the older, mature fish appear to grow more slowly. It is suggested that this discrepancy may be due to biased sampling of the old fish in the Bay of Fundy due to the segregation by size. The 0-class pollock found in the shallow, sublittoral zone feed mainly on algae-inhabiting organisms and to a lesser extent on plankton. The 1-year-olds in the same location have a similar diet but consume a greater proportion of planktonic animals. The larger, offshore pollock in the Bay of Fundy are predominantly plankton eaters, and the euphausiid *Meganyctiphanes norvegica* is by far the most important organism in the diet. On the Scotian Shelf and in the Laurentian Channel fish is the dominant type of food, except for the smallest sizes of pollock.

INTRODUCTION

The pollock, *Pollachius virens* (L.), is an Atlantic, amphiboreal species which has a western centre of abundance between Cape Cod and the Strait of Canso, and eastern centres of abundance in the waters surrounding Iceland, in the North Sea and off the western and northern coasts of Norway.

Although abundant in the Bay of Fundy region and the object of a fairly intense fishery for more than 100 years, it has been little studied. The fishing methods and grounds fished were summarized by Vladykov (1932), but with the introduction of new methods (artificial lures and otter trawls) since World War II the fishery has changed. The only available information on the biology of this species in the western Atlantic is in the statistical studies by Vladykov

[1]Received for publication November 16, 1962.
[2]Present address: Memorial University of Newfoundland, St. John's, Newfoundland.

J. Fish. Res. Bd. Canada, **20**(5), 1963.
Printed in Canada.

(1932) and Needler (1937), the growth studies by Mavor (1918), Rojo (1955, 1957), and Hoberman and Jensen (1962), the food studies of Kendall (1898), the length–weight studies of Craigie (1927), and the observations summarized by Bigelow and Schroeder (1953).

Much more work has been done in the eastern Atlantic: eggs and larvae were studied by Baranenkova (1957), Schmidt (1905, 1909); "harbour" pollock by Wollebæk (1900), Bertelsen (1942), Lie (1961); feeding by Nordgaard (1902), Wagner (1959); movements by Olsen (1956); age and growth by Saemundsson (1929), Fridriksson (1952, 1953, 1954, 1956, 1958) and Schmidt (1955, 1958, 1959), and the general biology by Mironova (1957, 1961).

The present paper summarizes observations made on the biology of the pollock in the western Atlantic, primarily in the Bay of Fundy area, during the summers of 1960 and 1961.

MATERIALS AND METHODS

Samples of large pollock were obtained from commercial landings, catches of the research vessels M. B. *Mallotus* and M. V. *Harengus*, a cruise on the commercial dragger M. V. *Sea Belle* in 1960 and two chartered trips on the dragger M. V. *Roxinda Ann* in 1961. The location of sampling areas is shown in Fig. 12.

"Harbour" pollock were collected at the Biological Station and other locations by means of baited lift-nets, shore seines and with hook and line.

The following information was recorded from each fish:

1. Length to the nearest centimetre, measured from the tip of the lower jaw to the centre of the tail fork;
2. Sex and Maturity: the gonads were examined visually and their sex and maturity recorded (p. 1301) using criteria similar to those of Powles (1958);
3. Food: the stomach contents were examined, the total volume and relative volume of the constituents recorded and in August 1961, the degree of digestion estimated. Contents of representative samples were preserved in 5% formalin for later examination. In the laboratory the total volume and the volumes of the constituents were determined by displacement, and the organisms identified with as much precision as was practical. (p. 1303);
4. Age Determination: otoliths were collected and stored dry. For the age readings the otoliths were broken and the number of hyaline zones counted from the nucleus out to the outer edge. (p. 1292).

Similar data obtained on the survey cruises of the M. V. *Harengus* and the C. G. S. *A. T. Cameron* on the Scotian Shelf and in the Gulf of St. Lawrence in 1957–61 were also utilized in the present study.

The distribution of pollock larvae in the Gulf of Maine is derived from various sources. The collections were made by 15-min horizontal plankton tows.

In the summer of 1960, one thousand fish were tagged with yellow Petersen disc tags attached to the dorsal musculature below the first dorsal fin.

DISTRIBUTION AND MOVEMENTS

Distribution and movements were studied to explore the subdivisions of the population. The terminology follows Marr (1957).

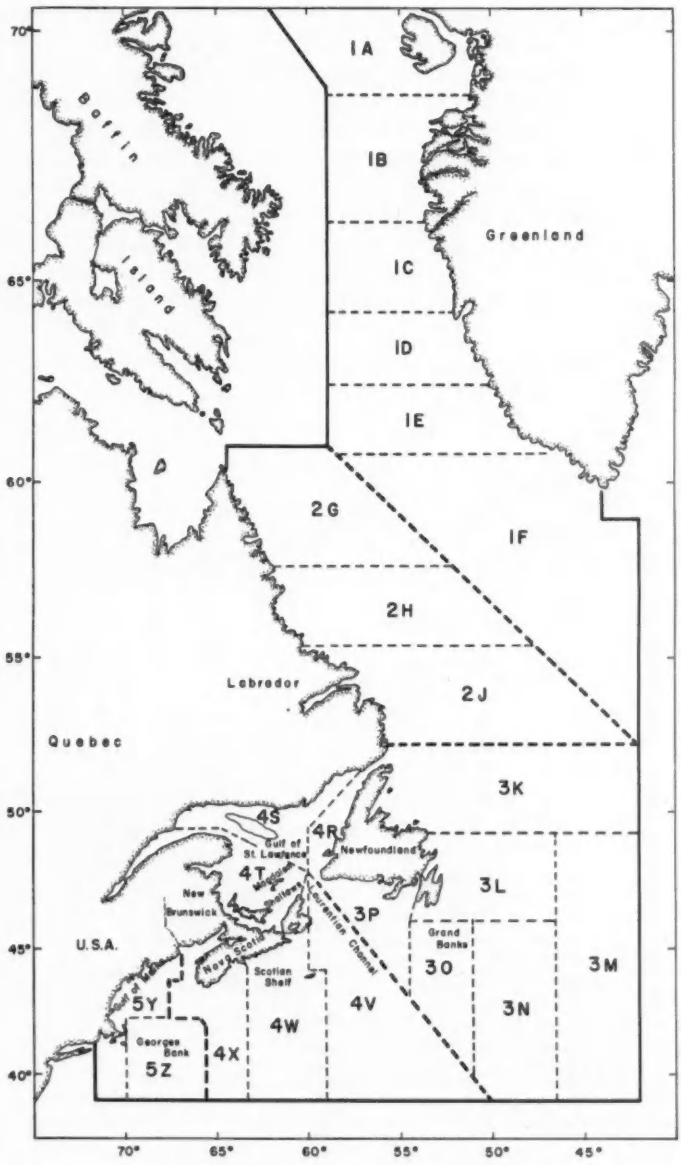


FIG. 1. International Commission for the Northwest Atlantic Fisheries Statistical Divisions and locations mentioned in the text.

Distribution

The distribution of the pollock in the western North Atlantic is shown in Fig. 2. This is based primarily on pollock catches reported from the International Commission for the Northwest Atlantic Fisheries (ICNAF) divisions (Fig. 1) in 1959 and 1960 (Table I; C. DeBaie, personal communication), and south of the Convention Area in 1958 and 1959 in the Statistical Digest of the United States Fish and Wildlife Service (Table II; Power, 1960, 1961), together with the Fisheries Statistics of Canada for 1956 and 1957 (1958, 1960), the ICNAF Statistical Bulletins (1954–61), Plate 59 of the Atlas of Canada (1957), and published records. The pollock ranges from North Carolina (Coles, 1926), Virginia (Table II) and Chesapeake Bay (Hildebrand and Schroeder 1928) north to southern Labrador (Table I; Thompson, 1932) and west Greenland (Table I;

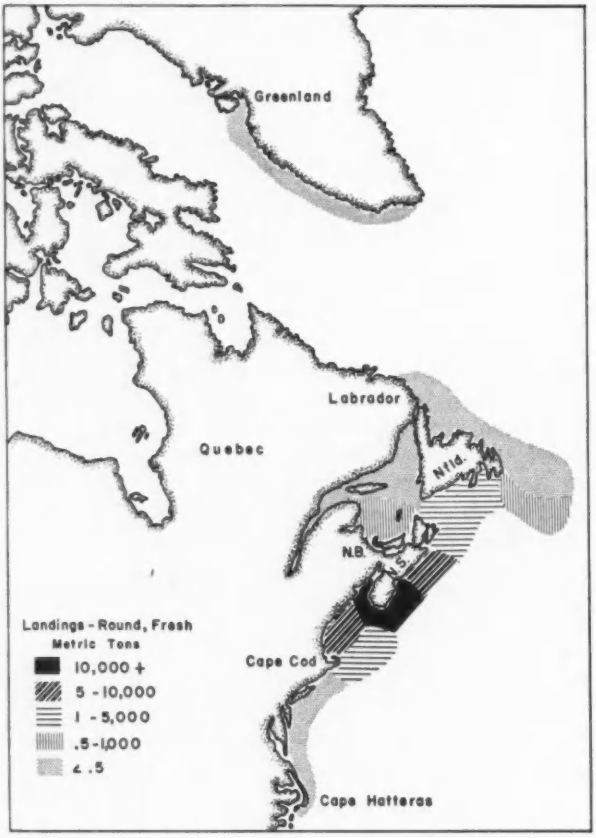


Fig. 2. Annual landings of pollock in the western North Atlantic (Tables I, II).

TABLE I. Pollock landings in ICNAF Divisions in 1959 and 1960 (metric tons, round fresh).

		Subarea 1							Subarea 2					Subarea 3							Subarea 4							Subarea 5			Total
		A	B	C	D	E	F	Total	G	H	I	J	Total	K	L	M	N	O	P	Total	R	S	T	V	W	X	Total	Y	Z	Total	
Canada	1959	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	8	141	484	637	23	17	140	1,905	8,531	12,709	23,325	1,389	–	1,389	25,351
	1960	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	16	144	495	657	5	–	56	804	9,312	18,239	28,416	2,211	–	2,211	31,284
Denmark	1959	–	–	–	–	–	–	52	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	52
	1960	–	–	–	–	–	–	13	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13
Germany	1959	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1
	1960	–	–	1	4	1	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6
Italy	1959	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	1960	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	2	–	–	4	1	–	–	5	–	–	–	7
Portugal	1959	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	737	98	–	835	–	–	–	836
	1960	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Spain	1959	–	–	–	–	–	–	–	–	–	–	–	–	–	48	–	472	151	2,747	3,418	4	4	470	1,760	52	–	2,290	–	–	–	5,708
	1960	–	–	–	–	–	–	–	–	–	–	–	–	153	27	–	347	267	3,370	4,164	–	–	8	584	199	–	791	–	–	–	4,955
U.K.	1959	–	50	–	–	–	50	100	–	–	–	122	122	–	47	–	–	169	173	388	–	–	–	–	–	–	–	–	–	–	610
	1960	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	339	657	996	16	–	–	–	–	–	–	–	–	–	1,012
U.S.A.	1959	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	6	2	12	3	1	1	45	1,137	1,667	2,854	3,891	4,319	8,315	11,181
	1960	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	149	1,785	1,946	4,334	3,834	8,186	10,132
Total:	1959	–	50	–	–	–	50	152	–	–	–	122	122	–	100	–	484	467	3,406	4,457	30	22	611	4,447	9,818	14,376	29,304	5,280	4,319	9,704	43,739
	1960	–	–	1	4	1	–	19	–	–	–	–	–	153	29	–	363	751	4,523	5,819	21	–	68	1,401	9,660	20,024	31,174	6,545	3,834	10,397	47,409

TABLE II. Pollock landings south of ICNAF Convention Area in 1958 and 1959 (metric tons, round fresh).

Year	Rhode Island	Conn.	New York	New Jersey	Delaware	Maryland	Virginia
1958	6	½	2	2	–	–	1
1959	12	–	4	½	–	–	1

Jensen and Hansen, 1931), but is only common between Georges Bank and southern Newfoundland. The largest landings are reported from the northern Gulf of Maine and off southwestern Nova Scotia (Division 4X).

In Canadian waters it is abundant in the summer and early autumn at the mouth of the Bay of Fundy where it is typically found on the slopes of shoals and banks. The pollock is also common on the Scotian Shelf, between and on the slopes of the banks. It is not abundant in the Gulf of St. Lawrence although it is a permanent resident of the Laurentian Channel where it has been taken as far west as Fox River (Steele, 1958), Ile Verte and Kamouraska (Vladykov and McAllister, 1961). In the Magdalen Shallows it is caught only in the summer and fall. It is rare on the eastern side of the Gulf of St. Lawrence (A. M. Fleming, personal communication) and has apparently not yet been recorded in the northern sector. The pollock is also caught in small quantities off southern Labrador, northern and eastern Newfoundland. It is apparently more numerous on the southern edge of the Grand Banks and off southern Newfoundland.

The distribution appears to be related to water temperatures, depth and feeding habits. Pollock are most abundant in the summer in Division 4X, where tidal turbulence assures relatively uniform water temperatures at all depths (6–13°C, Bigelow, 1928). Here pollock may be caught from the surface to 90 fathoms (165 m) or more, but most fish are caught on the slopes of shoals and banks at depths of 20–70 fathoms (35–130 m).

On the Scotian Shelf and in the Gulf of St. Lawrence the *A. T. Cameron* and M. V. *Harengus* also made their best catches on the slopes and in the channels between the banks at temperatures above 1.1°C (Fig. 3–7). This agrees with the observations of Mironova (1961) who reports that most catches of pollock in the Barents Sea are from water of 2–6°C and with the northern distribution limits in the western Atlantic. However, it does not explain the scarcity of pollock in the shallow water of the Magdalen Shallows or the Scotian Shelf at the same water temperatures as those of Division 4X. This difference in shoal-water distribution is probably related to the food which is carried over the shoals and banks by the turbulence in Division 4X.

SPAWNING AREAS

The distribution of ripe adults in the Gulf of Maine shows that spawning is restricted to the region off the mouth of Massachusetts Bay and between Cape Ann and the Isle of Shoals (Bigelow and Schroeder, 1953; Fig. 8). The ripe pollock are concentrated here in the spawning season (November–February) and become the object of an intensive fishery (Fish, 1928; Vladykov, 1932; Fig.

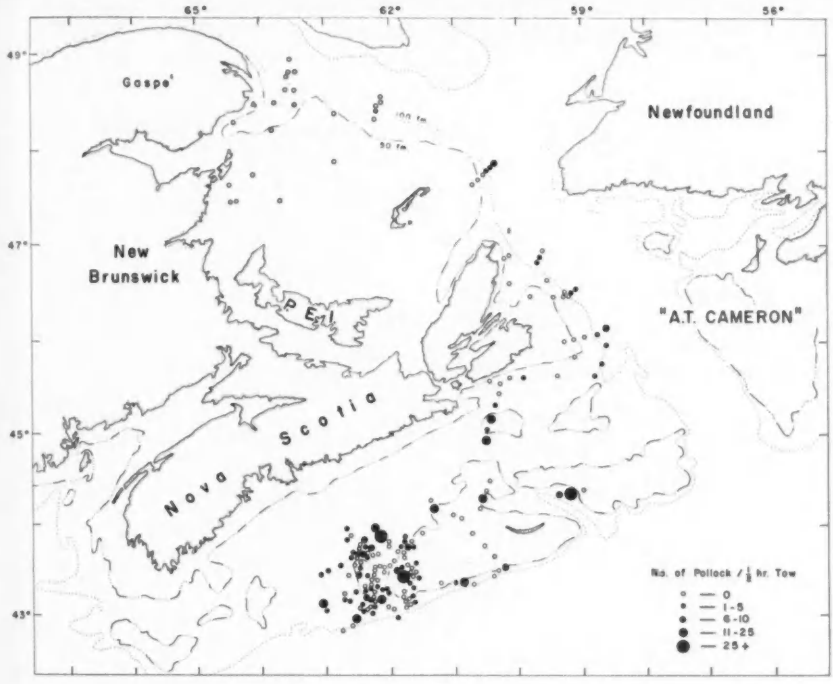


FIG. 3. Pollock catches on *A. T. Cameron* cruises 19, 20, 21 (January–March 1960).

13). Only a few ripe pollock have ever been collected in the rest of the Gulf of Maine, and none in the Bay of Fundy (Bigelow and Schroeder, 1953). The distribution of eggs and larvae coincides with the distribution of the ripe adults (Bigelow and Schroeder, 1953; Colton, personal communication; Fig. 9).

Little is known of possible spawning east of the Gulf of Maine due to lack of collecting in the proper season, but the following evidence suggests that spawning occurs there: (1) the presence of large, mature pollock off Nova Scotia in January and February (Fig. 3); (2) the catches of 9 ripe and ripening pollock on January 16–18, 1961, and 1 ripening pollock on January 24, 1960, off Cape Breton Island in 98–150 fathoms (175–275 m) by the *A. T. Cameron* show that at least a small amount of spawning occurs off Cape Breton Island (Fig. 8); (3) the distribution of pelagic larvae and juvenile pollock in relation to the non-tidal drift. The last point requires some amplification.

Figure 8, showing the surface circulation in the Gulf of Maine, on the Scotian Shelf and in the Gulf of St. Lawrence, uses information obtained from various authors. In the Gulf of Maine, as described by Bigelow (1928) for July and August, there is an almost closed system — the anti-clockwise Gulf of Maine eddy — but with some water entering from the east and leaving to the south. Bigelow regarded this pattern as permanent, but recent studies by Day (1958),

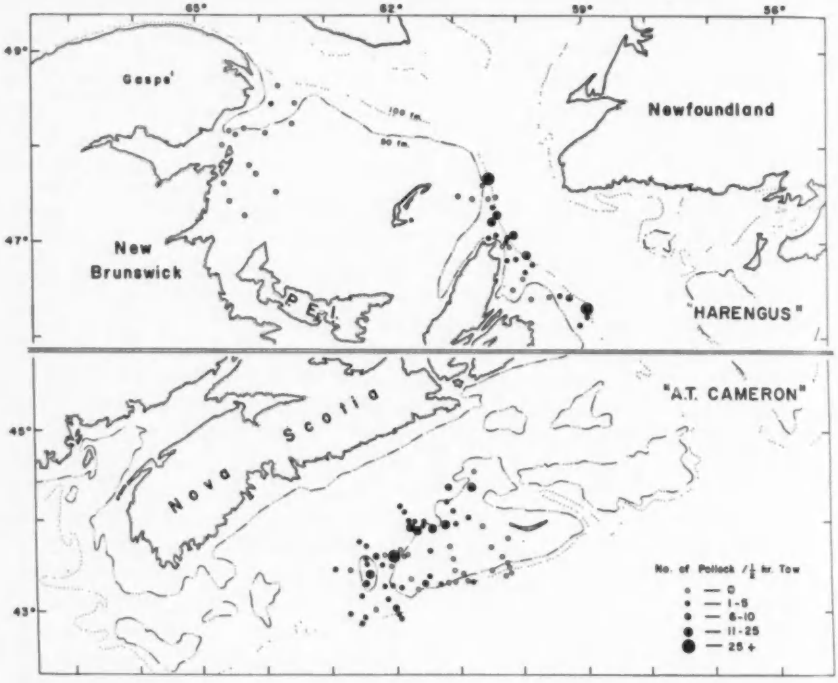


FIG. 4. Pollock catches on *Harengus* cruises 9, 12 (May–June 1959) and *A. T. Cameron* cruise 37 (April–May 1961).

Bumpus (1960) and Colton and Temple (1961) suggest that it is subject to yearly and seasonal variations. The drift-bottle recoveries studied by these authors suggest that the eddy becomes restricted to the northern half of the Gulf of Maine under the influence of the dominant offshore winds in late winter and spring (late February–April), and that in the south the dominant flow is southerly and toward the edge of the continental shelf. They conclude that eggs and larvae released in the southern Gulf of Maine will be swept away. Unfortunately, little is known of the circulation from November to February when pollock spawning is at its height. According to Day (1958), the flow over the spawning grounds in late February is southerly and out of the Gulf of Maine. On the other hand, some of the drift bottles released over the spawning grounds in early February by Fish (1928) were recovered on the shores of Nova Scotia as well as south of Cape Cod, showing that the Gulf eddy was present and would have retained some of the eggs and larvae inside the Gulf of Maine at that time. It can be concluded therefore that at least in some years pollock larvae from the spawning grounds at the mouth of Massachusetts Bay would be kept in the Gulf of Maine, as well as drifted west of Cape Cod or lost in the open sea.

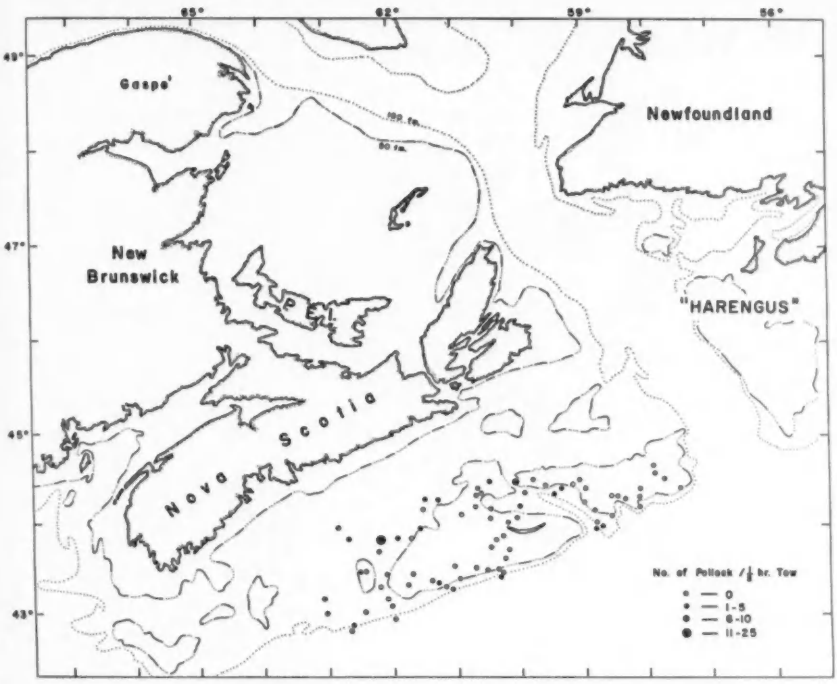


FIG. 5. Pollock catches on *Harengus* cruise 13 (July 1959).

Off Nova Scotia the surface circulation consists of an offshore, anti-clockwise eddy centred near Sable Island, and an inshore, westerly continuation of the Cape Breton current, which enters the Gulf of Maine off western Nova Scotia. This system is important since it would prevent eggs and larvae from the Gulf of Maine reaching inshore Nova Scotian waters and supply young pollock to the Gulf of Maine from spawning on the Scotian Shelf.

The distribution of pollock larvae is known only for the Gulf of Maine (Fig. 9, 10). In January and February the catches of pollock larvae of the research vessels *Delaware*, *Albatross III* (Colton, personal communication), and *A. T. Cameron* cruises were concentrated in the southern Gulf of Maine and south of Cape Cod, although tows were made in all sections of the Gulf of Maine. At the same time, the cruises of the Passamaquoddy survey in the northern part of the Gulf of Maine (table I in Legaré and Maclellan, 1960) collected no pollock larvae (Maclellan, personal communication).

A few small larvae were collected at the Lurcher Lightship (43°48′30″N, 66°31′45″W) during the winter of 1959–60 (Fig. 9; Table III). These larvae could have come from either the southern Gulf of Maine or from possible spawning on the Scotian Shelf. Since the incubation of pollock eggs takes from 6 to 12 days and the absorption of the yolk 5 days at the prevailing surface temperatures

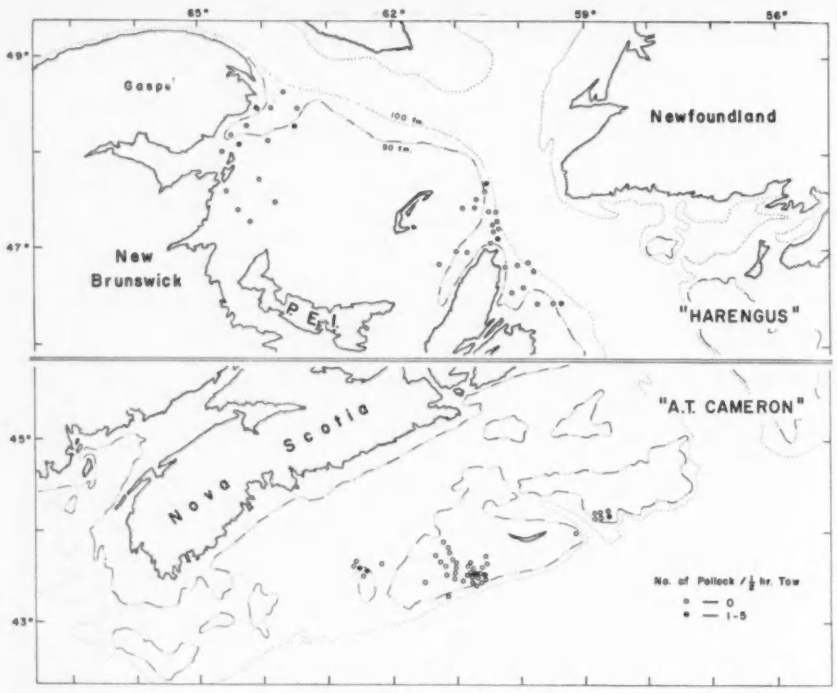


FIG. 6. Pollock catches on *Harengus* cruises 17, 18 (October–November 1959) and *A. T. Cameron* cruise 30 (September–October 1959).

of the Gulf of Maine (Bertelsen, 1942; Bigelow and Schroeder, 1953), it is concluded that the larvae collected at the Lurcher Lightship were only 2–3 weeks old when caught. According to the estimates of Redfield (1939) the Gulf of Maine eddy would take at least 6 weeks to transport larvae from the mouth of Massachusetts Bay to the Lurcher Lightship. Thus it seems more probable that these young had been spawned off Nova Scotia.

The March, April and May collections of larvae and juvenile pollock in the Gulf of Maine (Fig. 10) were scattered throughout the Gulf of Maine as well as south and east of Cape Cod. This distribution suggests that they were spawned in the southern Gulf of Maine and retained by the Gulf eddy.

When the young pollock are about 3 cm long they move into the shallow, sublittoral zone for their first 2 years. At this time they are known as "harbour" pollock. Since it is unlikely these small fish migrate long distances, their distribution reveals something of the drift of the young and the probable location of spawning areas in regions where eggs and larvae have not been collected. "Harbour" pollock have been observed from the Maine border east to Cape Breton Island and southern Newfoundland, but are rare or absent in the Gulf of St. Lawrence and on the west, north and east coasts of Newfoundland (Fig. 11).

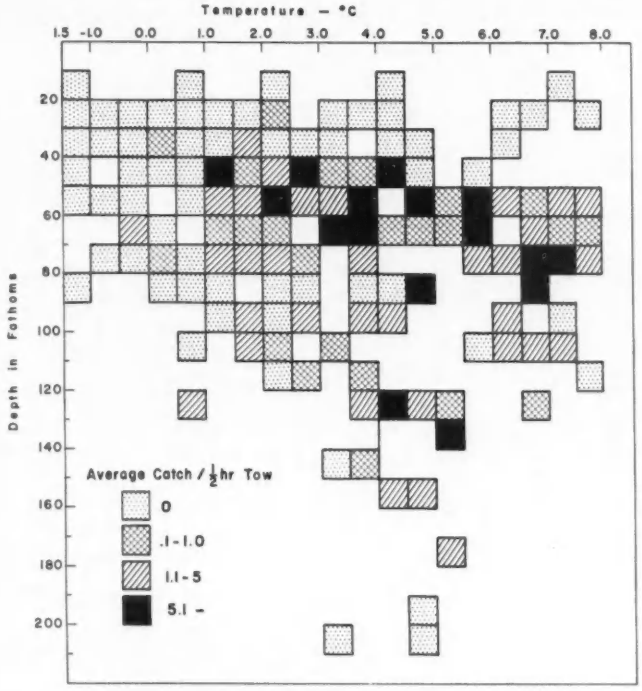


FIG. 7. Catches of pollock (numbers per half-hour tow) made on the Scotian Shelf by the *A. T. Cameron* at different depths and temperatures; all seasons combined.

TABLE III. Pollock larvae collected at the Lurcher Lightship.

Collection No.	Date	No.	Size range	Remarks
			mm	
52	Dec. 27, 1959	1	4	Yolk absorbed
56	Jan. 10, 1960	6	4	" "
61	Jan., 1960	1	5.5	" "

It is unlikely that the "harbour" pollock of Nova Scotia and southern Newfoundland have drifted from the southern Gulf of Maine, as the dominant inshore current moves in the opposite direction. If they were to drift to Nova Scotia, they would have to enter the northward-moving slope water, and later leave it and cross the coastal water to reach the shores of Nova Scotia and southern Newfoundland. The southerly drift in the Gulf of Maine could carry the larvae

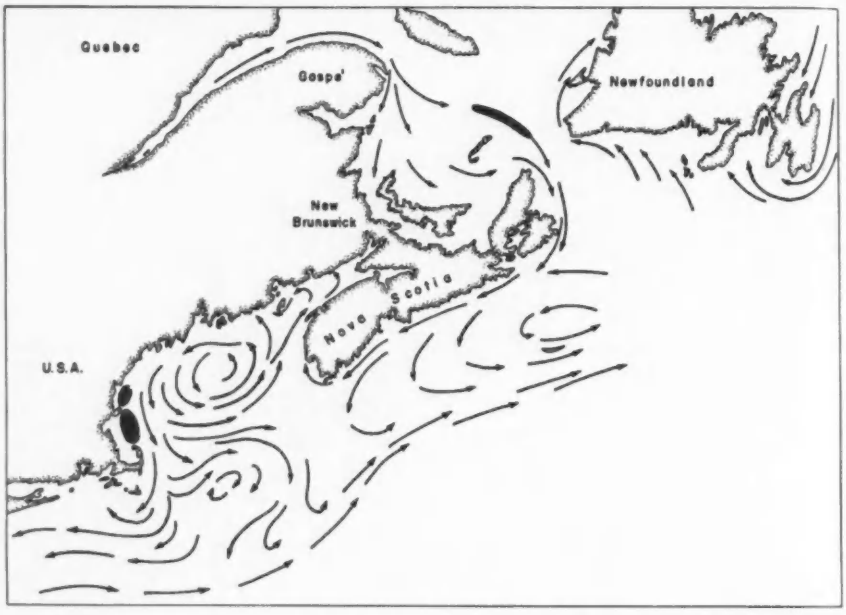


FIG. 8. Pollock spawning areas and non-tidal summer surface currents of western Atlantic coastal waters (redrawn with modifications from Bigelow (1928), Colton and Temple (1961), Sandstrom (1919), and Trites and Banks (1958)).

into the slope water (Colton and Temple, 1961), but a return to the coastal water seems very unlikely. Thus, there is evidence that pollock spawn on the Scotian Shelf as well as at the mouth of Massachusetts Bay, and that the young found at the mouth of the Bay of Fundy may come from either spawning ground.

POLLOCK MOVEMENTS

Commercial catches of pollock in the Gulf of Maine (Fig. 12) show marked seasonal variations (Fig. 13). In the northern Gulf of Maine, where pollock do not spawn, the landings are largest from June to October when the fish are in the recovering and ripening phases of the reproductive cycle. The catches in the southern Gulf of Maine are largest from October to February when the pollock are spawning. These reciprocal variations in landings suggest that the fish caught in the northern Gulf of Maine in the summer migrate south and spawn in the southern Gulf of Maine in the winter.

To learn something of the movements of the Bay of Fundy pollock, 1000 fish were tagged in July 1960. Otter-trawl-caught fish were tagged at first, but they were in such poor condition that only 9 were released. With the exception of 69 large specimens (65–85 cm) caught in a weir at North Head, Grand Manan, the rest were caught with handlines by commercial fishermen.

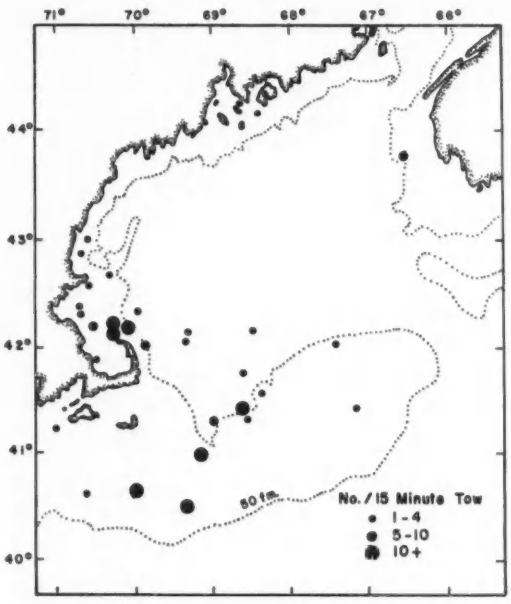


FIG. 9. January and February catches of pollock larvae in the Gulf of Maine. Cruises: *Delaware* 57–1 and *Albatross III* 88 (January and February 1957), Marak (personal communication); *A. T. Cameron* 3 (January 1959); Lurcher Lightship (January 1960).

Of the latter, 498 were large fish (65–85 cm) which were released in the "River" (between Deer Island and Campobello Island); the remaining 424 were of medium size (60–75 cm) and were released off northern Grand Manan.

The returns to date (August, 1962) are summarized in Table IV and plotted in Fig. 14.

From July to November 1960 most recaptures were made in the Bay of Fundy area and off southwestern Nova Scotia, but in November, December and January recoveries also came from the spawning grounds at the mouth of Massachusetts Bay. The few returns from March and April 1961 were from off southwestern Nova Scotia. From May to November 1961 they were again confined to the Bay of Fundy region, with many from the original tagging areas. Two, however, were from the "Western Hole" (between Browns and Little Lehave Banks) where a large concentration of pollock was fished intensively during June and July. In December 1961 and January 1962 recoveries again came from the spawning ground at the mouth of Massachusetts Bay. The few recoveries in the summer of 1962 were from the Bay of Fundy.

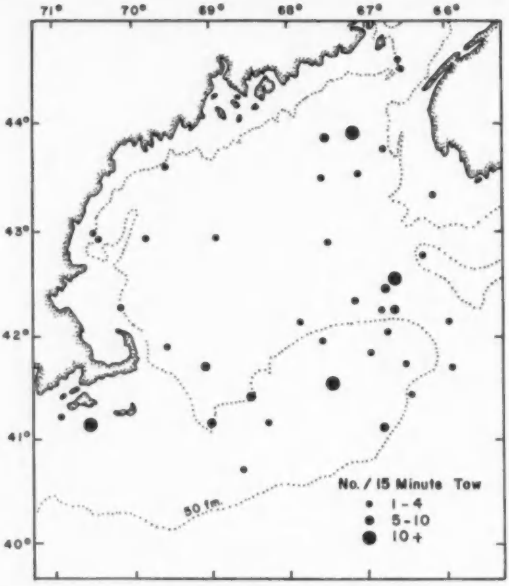


FIG. 10. March–May catches of pollock larvae in the Gulf of Maine. Cruises: *Albatross III* 46, 48—1953 (Marak and Colton, 1961); *Albatross III* 57, 58, 60, 61—1955 (Marak *et al.*, 1962); *Albatross III* 72, 73, 75, 76—1956 (Marak, personal communication).

Even allowing for the seasonal nature of the fishery in both the southern and northern halves of the Gulf of Maine, recoveries show that some of the pollock found in the Bay of Fundy region during the summer migrate south to the spawning grounds of the southern Gulf of Maine in the winter. It is also possible that pollock migrate to the region south of western Nova Scotia in the winter as do the haddock (McCracken, 1960), and as the recoveries from off southwestern Nova Scotia in autumn and spring seem to suggest.

Few pollock are caught south of western Nova Scotia during the winter spawning period. However, during the early summer of 1961 when most of the pollock landed came from a large concentration in the "Western Hole" south of western Nova Scotia (4XO, 4XN), only 2 returns came from there. This suggests that there is relatively little mixing of the fish of the Bay of Fundy with those of the Scotian Shelf, at least during the summer.

Bigelow and Schroeder (1953) demonstrated from tagging studies that the pollock that occur in the southern Gulf of Maine in summer showed little movement. It can be tentatively concluded therefore that there are 3 groups of pollock in the Gulf of Maine and adjoining regions in summer: (1) the Bay of

TABLE IV. Returns and reports[a] of tagged pollock, 1960–62.

Tagging area:		"River" (Handline)			North Head (Handline)			North Head (Weir)		
No. released:		498			424			69		
		Tagging area returns	Distant[b] returns	Total reports	Tagging area returns	Distant[b] returns	Total reports	Tagging area returns	Distant[b] returns	Total reports
1960	July	3	0	3	0	1	1			
	August	19	1	20	0	2	3	0	2	2
	September	7	0	7	0	1	1	0	1	1
	October	3	2	5	0	9	9	0	1	1
	November	8	5	13	1	4	6	0	1	1
	December	0	3	3	0	1	2	0	0	0
1961	January	0	0	0	0	3	3	0	0	0
	March	0	3	3	0	1	1	0	0	0
	April	0	1	1	0	0	0	0	1	1
	May	3	0	3	0	2	2	0	0	0
	June	11	0	11	0	3	3	0	2	2
	July	2	0	2	0	6	7	0	0	0
	August	0	1	1	0	3	3	0	2	2
	September	1	2	3	0	1	1	0	0	0
	October	0	0	0	0	1	1	0	0	0
	November	0	0	0	0	2	4	0	0	0
	December	0	1	1	0	1	1	0	0	0
1962	January	0	1	1	0	0	0	0	0	0
	March	0	0	0	0	1	0	0	0	0
	May	0	1	1	0	0	0	0	0	0
	June	1	0	0	0	0	0	0	1	1

[a]Terminology after the recommendations of ICNAF Standing Committee on Research and Statistics (ICNAF 1961).
[b]More than 10 miles from tagging area.

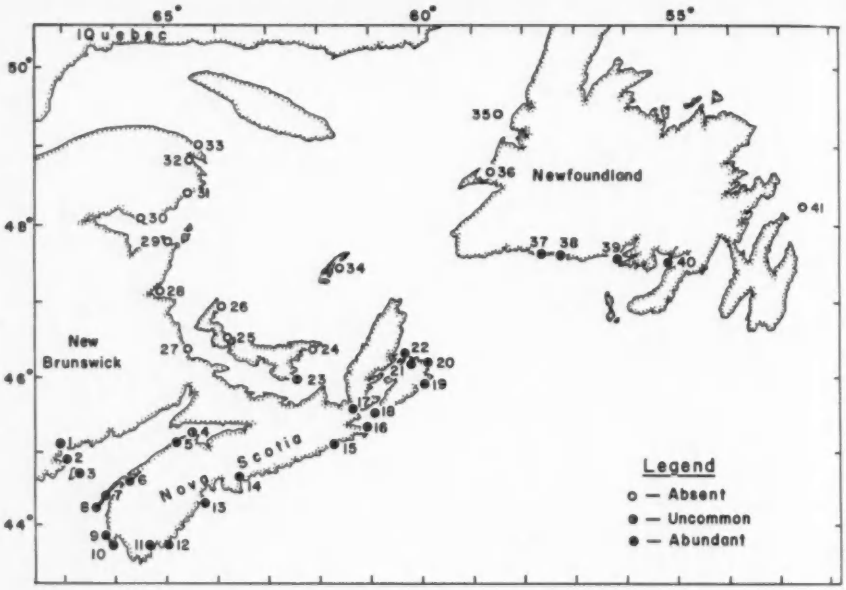


FIG. 11. Distribution of "harbour" pollock in eastern Canadian waters. 1. St. Andrews, 2. Campobello Island, 3. North Head, Grand Manan, N.B. (personal observation); 4. Scotsman Bay, N.S. (Bousfield and Leim, 1960); 5. Hall's Harbour, N.S. (Y. Jean, personal communication); 6. Digby, 7. East Ferry, 8. Freeport, N.S. (D. Fitzgerald and M. Fraser, personal communication); 9. Sandy Point, 10. Little River, 11. Sandy Point and Shelburne, 12. Lockeport, 13. Lunenburg, N.S. (M. Fraser, personal communication); 14. Halifax, N.S. (G. Sullivan, personal communication); 15. Port Bickerton, 16. Canso, N.S. (G. DeLouchry, personal communication); 17. Port Hawkesbury, N.S. (personal observation); 18. Petit de Grat, 19. Louisbourg, 20. Glace Bay, 21. North Sydney, 22. Alder Pt., N.S. (R. MacPherson, personal communication); 23. Muray Hbr., 24. Souris, P.E.I. (G. Sullivan, personal communication); 25. Malpeque Bay, P.E.I. (Needler, 1940); 26. Tignish, P.E.I. (Cornish 1912); 27. Buctouche, N.B. (A. Maillet, personal communication); 28. Miramichi estuary (McKenzie, 1959); 29. Caraquet, N.B., 30. New Carlisle, 31. Grand River, 32. Gaspé, 33. Fox River, P.Q. (personal observation); 34. Magdalen Islands, P.Q. (J. Bergeron, personal communication); 35. East coast of Newfoundland, 36. Port au Port, 37. Burgeo, 38. Ramea, 39. Hermitage Bay, 40. Fortune Bay, 41. St. Mary's Bay–Notre Dame Bay, Nfld. (A. M. Fleming, personal communication).

Fundy fish, (2) the group of fish found south of western Nova Scotia, and (3) the southern Gulf of Maine pollock. How distinct these groups are cannot be determined from the present study.

The migration of pollock away from the Bay of Fundy region in the winter is probably related to the difficulties of successful reproduction in the northern Gulf of Maine. The young, immature fish remain in the north and have been caught in large quantities upon occasion (Martin, 1960). Failure to reproduce

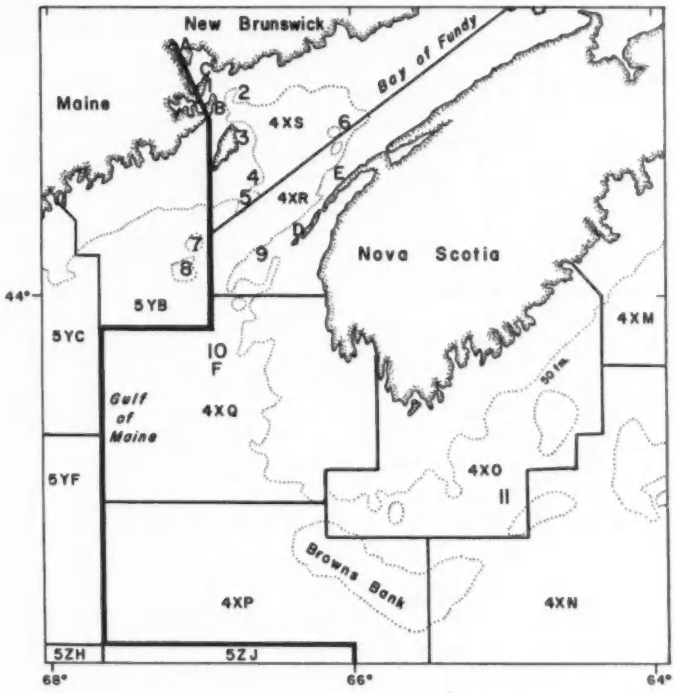


FIG. 12. Bay of Fundy region showing where samples were obtained and Statistical Unit Areas. *Large pollock*: 1. "River" (between Deer and Campobello Islands); 2. Wolves Bank; 3. Inshore North Head; 4. "Gravelly"; 5. "Soundings"; 6. Yankee Bank; 7. Northeast Bank; 8. Southwest Bank; 9. "Rip"; 10. Pollock Shoal; 11. Western Hole. "*Harbour pollock*: A. St. Andrews; B. Campobello Island; C. Bliss Island; D. Freeport; E. Sandy Cove; F. Pollock Shoal.

in the northern Gulf of Maine is found in many other animals with pelagic eggs and larvae: hake, haddock, cod, mackerel (Huntsman, 1918a, 1952), rockling (Battle, 1930), plaice (Huntsman, 1918b), cunner and lobster (Huntsman, 1923), *Sagitta elegans* (Huntsman and Reid, 1921), *Calanus finmarchicus* (Fish, 1936a), *Pseudocalanus minutus* (Fish, 1936b) and *Oithona similis* (Fish, 1936c). The reason for this failure of reproduction even in organisms which spawn in the area is obscure, although Huntsman (1918a, 1952) has suggested that it is due to the strong tides in the northern Gulf of Maine. The resulting low surface temperature (Huntsman, 1923) or mechanical shocks due to turbulence could prevent normal development of the eggs.

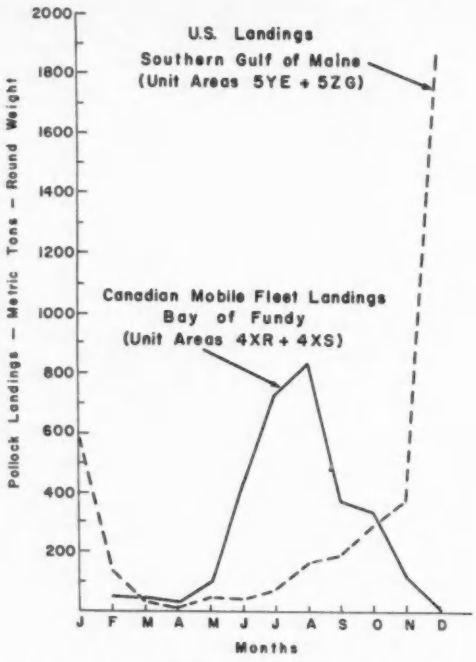


FIG. 13. Seasonal distribution of pollock landings in the Gulf of Maine, 1961.

DISTRIBUTION ACCORDING TO SIZE AND AGE

"HARBOUR" POLLOCK

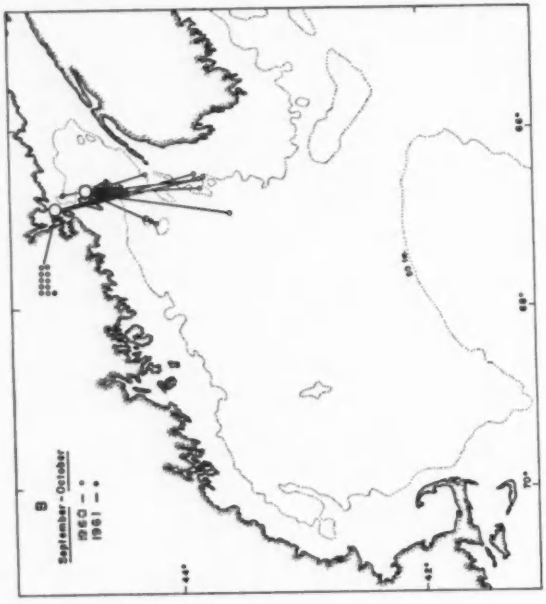
The 0-pollock move inshore from April to June at a size range of 2.5–3.5 cm (Bertelsen, 1942; Lie, 1961) in European waters, but it is not known exactly when or at what size this movement takes place in North American waters. Since spawning occurs earlier, it could take place as early as late March when juveniles of 2.5 cm occur in the plankton in the Gulf of Maine (Marak and Colton, 1961; Marak *et al.*, 1962). By late May and early June the invasion may be completed since the juveniles are no longer caught in the plankton (Marak and Colton, 1961). The earliest collection at the Biological Station, St. Andrews, N.B., was made on June 21, 1946.

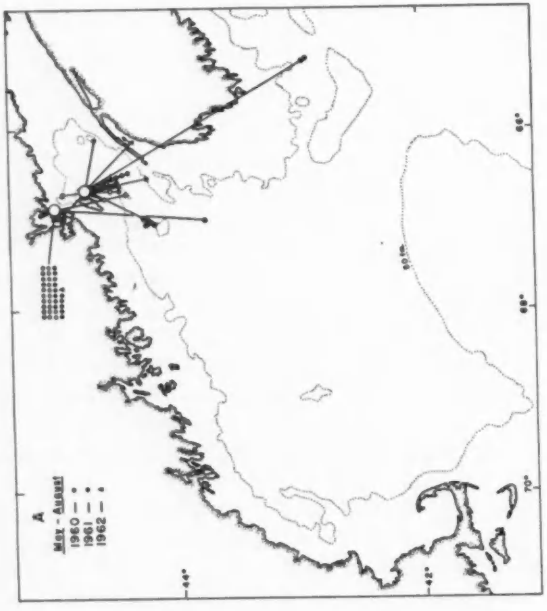
These 0-fish remain inshore during the summer but spend the winter offshore in large pelagic shoals. There is no information available on fish for this season other than that during a period of herring scarcity from 1951 to 1958 large quantities of small pollock were seined at the mouth of the Bay of Fundy from January to April (Martin, 1960). This suggests that extensive movements are not undertaken by these small fish.

TABLE V. Pollock catches by 4 selected otter trawlers with landings (metric tons, round fresh) and tag recoveries of all mobile vessels in 1961 for Bay of Fundy and Nova Scotia fishing areas.

	Bay of Fundy (4XR + 4XS + 5YB)												Western Nova Scotia (4XQ)				Southern N.S.(4XO+4XN)			
	Estimated catches on fishing grounds by 4 draggers										Total mobile fleet		Est. catch by 4 draggers		Total mobile fleet		Est. catch by 4 draggers		Total mobile fleet	
	SW Bank		NE Bank		Yankee B.		Gravelly		Soundings		Landings	Tag rec.	Pollock Shoal		Landings	Tag rec.	Western Hole		Landings	Tag rec.
Month	Hrs	Est. catch	Hrs	Est. catch	Hrs	Est. catch	Hrs	Est. catch	Hrs	Est. catch			Hrs	Est. catch			Hrs	Est. catch		
Feb.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mar.	10½	2	18	16	0	0	0	0	0	0	18	0	146	148	180	4	0	0	0	0*
Apr.	0	0	10	1	0	0	0	0	0	0	14	0	35½	22	39	1	0	0	0	0
May	20	5	4	1	0	0	0	0	0	0	40	2	16½	11	165	0	218	276	222	0
June	0	0	38	37	0	0	0	0	0	0	133	3	0	0	80	0	288	472	1060	0
July	8½	3	77	97	21	43	0	0	6	9	274	4	7½	8	10	0	276	753	950	2
Aug.	9	2	21	12	11	3	15	20	117	148	618	3	1	½	0	1	0	0	540	0
Sept.	30	13	43	12	0	0	32	13	110	114	261	3	4	2	1	0	0	0	0	0
Oct.	0	0	184	144	0	0	23	13	21	5	28	1	0	0	0	0	0	0	0	0
Nov.	0	0	0	0	0	0	8	0	26	2	6	2	0	0	0	0	0	0	0	0
Dec.	0	0	0	0	0	0	4	0	0	0	1	0	0	0	0	0	0	0	0	0
Total:	78	25	395	320	32	46	82	46	280	273	1393	18	280½	191½	475	6	782	1501	2772	2

*One recovery by U.S. boat.


B
September - October
1960 — •
1961 — •
70°
65°
60°
55°
50°
45°
40°


A
May - August
1960 — •
1961 — •
1962 — •
70°
65°
60°
55°
50°
45°
40°

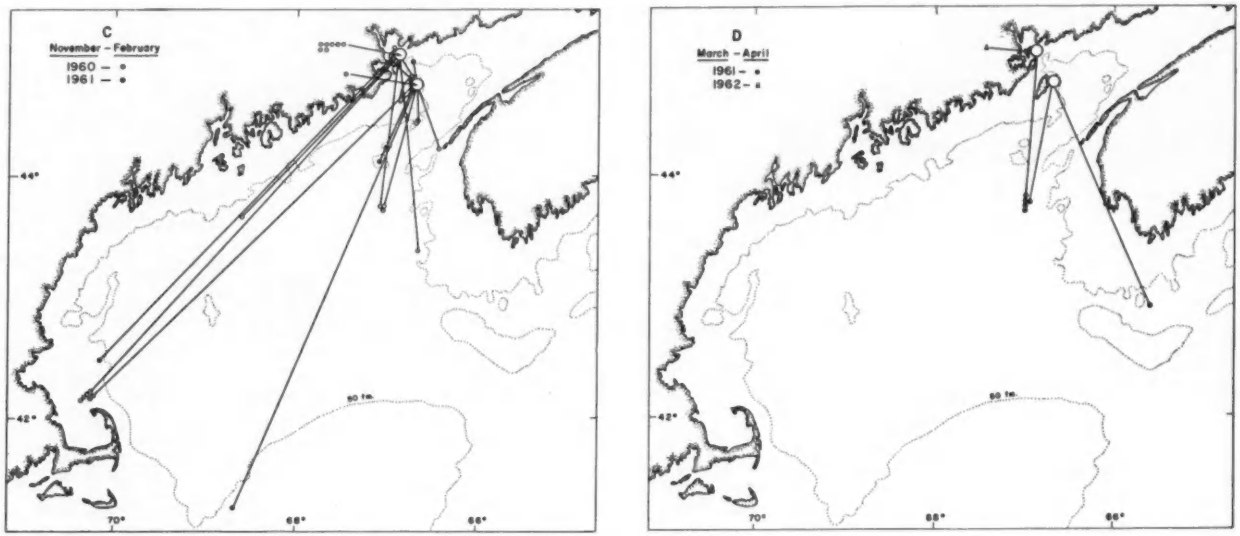


FIG. 14. Pollock tag returns, 1960–1962. A. Summer; B. Autumn; C. Winter; D. Spring.

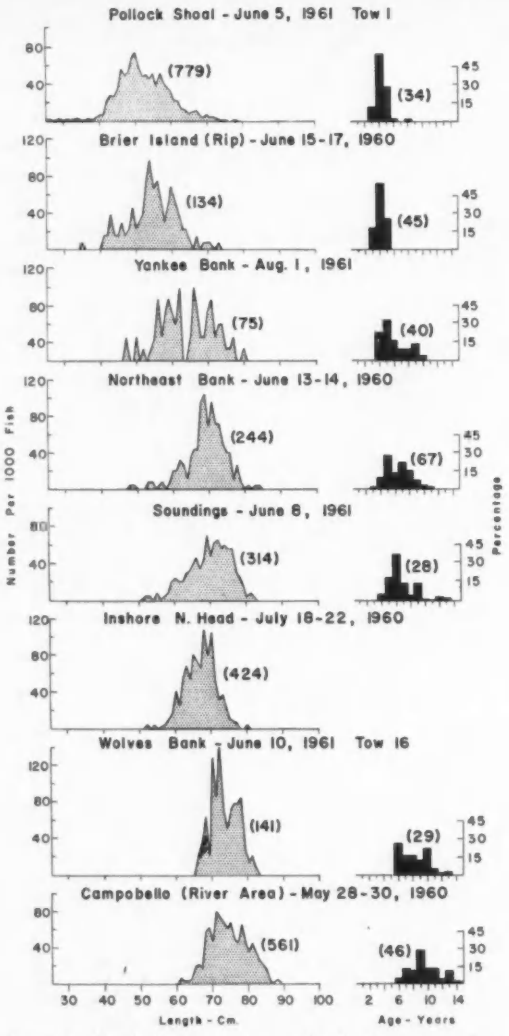


FIG. 15. Typical size- and age-distributions of catches from the Bay of Fundy (numbers of fish in parentheses).

According to Bigelow and Schroeder (1953) these fish, now 1 year old, reinvade the sublittoral zone in the following April, but they do not mingle with the 0 year-class, remaining in separate schools and typically in slightly deeper water. They disappear from the shallow, sublittoral zone in early August when 20–25 cm in length and probably move into deeper water.

Little is known of the behaviour of the 2-year-old fish. Mavor (1918) was able to catch specimens (30–47 cm) with a beach seine in shallow water off

Campobello in August 1916. None could be caught with a seine at the same location in 1960, but 2 specimens (33–34 cm) were taken nearby in shallow water with hook and line. These observations suggest that the 2-year-olds inhabit slightly deeper water offshore than the 0- and 1-year-old fish. On the other hand, many 2-year-old pollock (mean length 31 cm) were caught on the Pollock Shoal in 70–80 fathoms (130–150 m) of water in June 1960, showing that they may appear offshore.

Offshore Pollock

Bay of Fundy. Large fish (65–85 cm, 6–11 lb, 6–11 years old (Fig. 15)) were caught on Wolves Bank in June 1960 and in June and August 1961, in the "River" in 1960 and 1961 (also reported for the same area in 1915 and 1916), and in a weir at North Head, Grand Manan, in 1960. Fish of this size range are

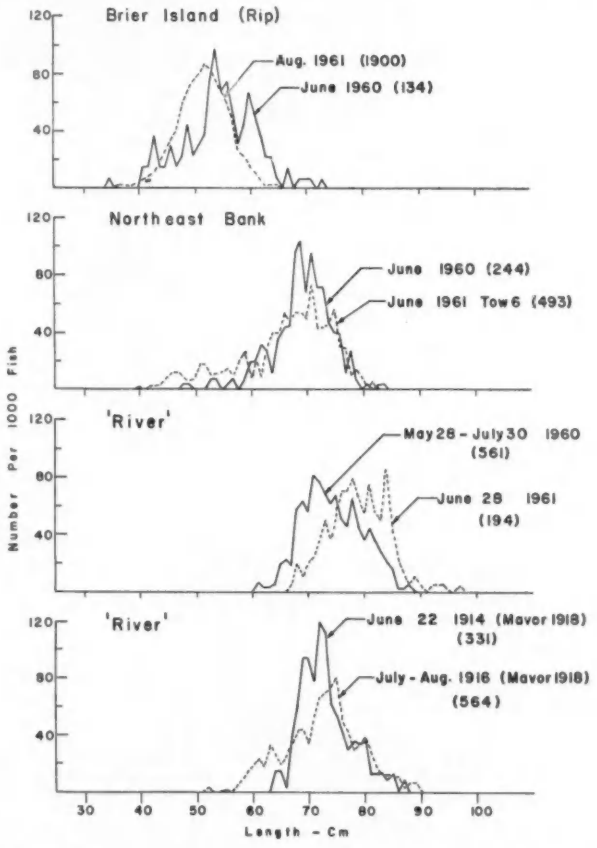


Fig. 16. Seasonal and yearly variations in size distributions in the Bay of Fundy (numbers of fish in parentheses).

therefore typical of the Wolves Bank–"River" area during the summer. Returns of those tagged in the "River" area during the summer of 1960 were mainly restricted to the area of tagging except in the autumn and winter when they also came from off western Nova Scotia and the southern Gulf of Maine.

Fish of medium size (60–75 cm, 4–8 lb, 5–7 years old (Fig. 15)) were taken on Northeast Bank in June of 1960 and 1961, on the Soundings in July 1960 and June and August 1961, inshore North Head in July 1960, on the Gravelly in August 1961, and on Yankee Bank in August 1961. They were distributed across the mouth of the Bay of Fundy. Recoveries of pollock of this size range tagged off North Head came from all the above grounds in the summer months, suggesting that they move freely from one ground to another, unlike those of the "River" area. Few returns came from the northern Wolves Bank–"River" area inhabited by the large fish.

Small fish (45–60 cm, 1–4 lb, 3–5 years old (Fig. 15)) were taken on the Pollock Shoal in June and August 1961, on the "Rip" in June 1960 and June and August 1961, and on Northeast Bank in June 1961. Even smaller fish (28–45

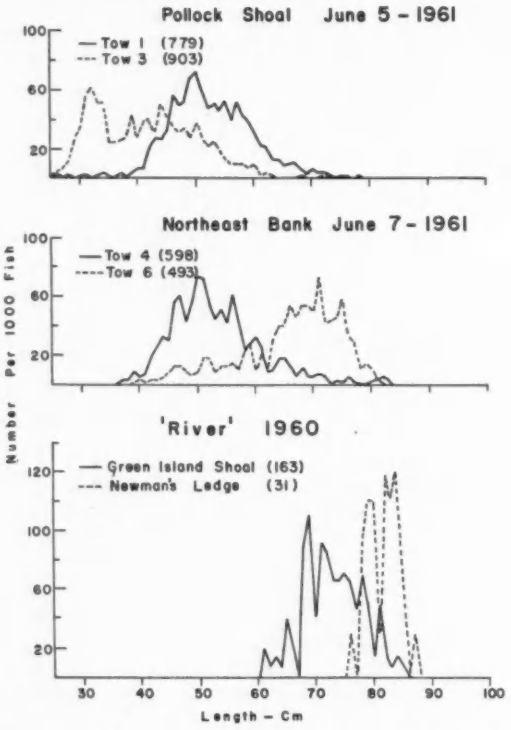


FIG. 17. Variations in size compositions on Pollock Shoal, Northeast Bank and in the "River" (numbers of fish in parentheses).

cm, ½–2 lb, 2–4 years old (Fig. 17)) were caught in one tow on the Pollock Shoal in June 1961. Thus, these small fish appear to be restricted to the area off western Nova Scotia.

There appears to be a general tendency for segregation by size and a gradient in the size ranges of the pollock in the Bay of Fundy, with the smallest fish found off western Nova Scotia and the largest in the Wolves Bank–"River" area. This is shown in Fig. 15, but it should be emphasized that samples included in this

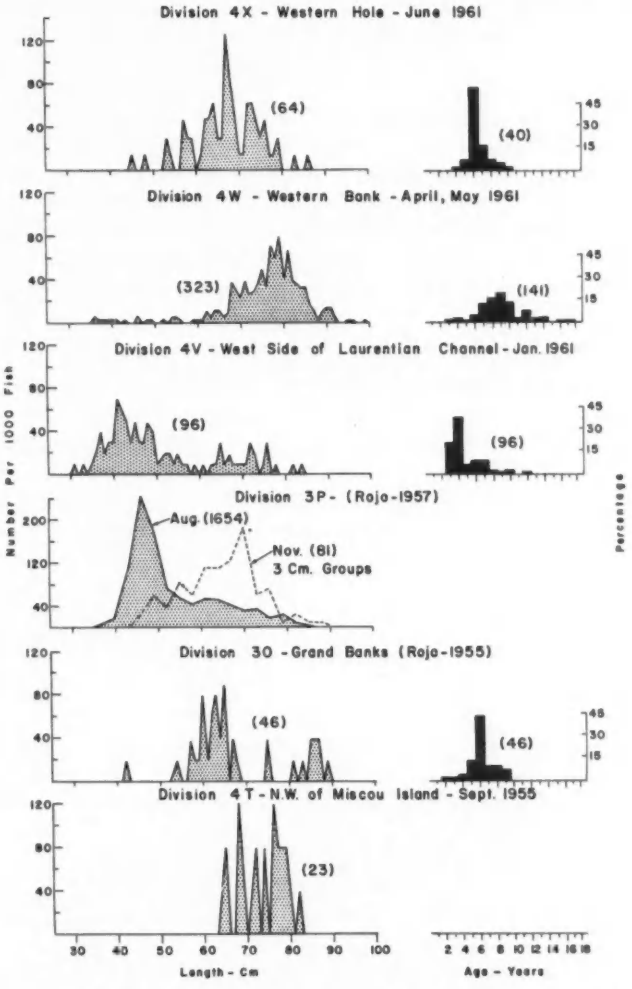


FIG. 18. Size- and age-compositions of catches from off Nova Scotia, off Newfoundland and in the Gulf of St. Lawrence (numbers of fish in parentheses).

figure were selected in some areas to provide the best gradient. Since this pattern has been observed during several years (Fig. 16), it is probably a characteristic feature of the summer pollock distribution in the Bay of Fundy. A somewhat similar gradation was reported for the cunner (*Tautogolabrus adspersus*) in the Bay of Fundy by Huntsman (1918a).

On the Pollock Shoal, Northeast Bank and in the "River" catches with different size distributions were made on the same ground (Fig. 17). This shows that segregation by size is an important feature of pollock behaviour even in a small area. Such schooling makes it difficult to obtain representative samples from the whole population for estimating year-class strengths and growth rates of pollock.

OTHER AREAS. The size compositions of samples from other areas are shown in Fig. 18. Medium to large fish were taken on the Scotian Shelf, on the Grand Banks and in the Gulf of St. Lawrence, but small fish (40–55 cm) were caught in the vicinity of the Laurentian Channel. Therefore, there may be a gradient of sizes off Nova Scotia comparable to that described for the Bay of Fundy.

A similar situation appears to exist off Iceland where medium fish are caught off the north coast (Fridriksson, 1952, 1956) and large fish off the southwest coast (Schmidt, 1958).

GROWTH

"HARBOUR" POLLOCK

Growth of small "harbour" pollock was studied by comparing size compositions of collections made in different seasons (Petersen method) and by counting the hyaline zones of the otoliths. The mean lengths of the samples (Table VI) are plotted in Fig. 19, together with data from western Norway (Lie, 1961) and

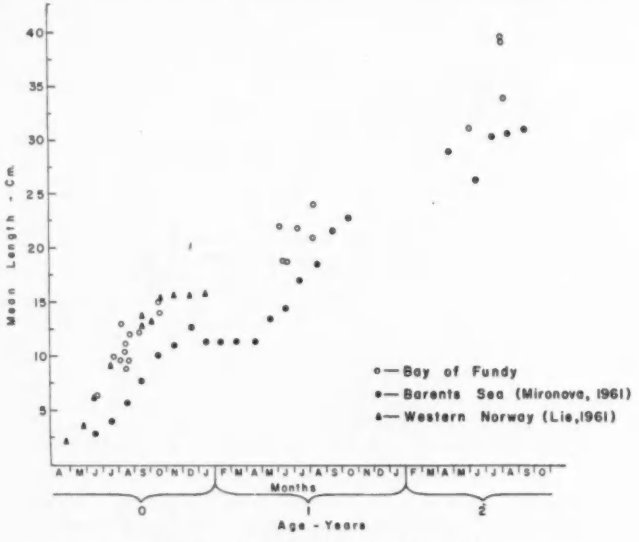


FIG. 19. Growth of "harbour" pollock.

TABLE VI. Collections of "harbour" pollock.

Year-class	Date	No.	Mode	Mean length	Range	Location	Means of capture
			cm	*cm*	*cm*		
0	21/6/46	4	–	6.5	5–7	St. Andrews, N.B.	Unknown
	22/7/46	10	10.5	10.0	8–11	St. Andrews, N.B.	Unknown
	4/8/16	19	9	9.7	7–11	Campobello Is.	Shore seine (Mavor, 1918)
	3–4/8/16	7	–	13.0	11–15	St. Andrews, N.B.	Hook and line " "
	8–9/8/60	302	10	10.5	9–12	St. Andrews, N.B.	Lift net
	11/8/60	4	–	9	8–11	Campobello Is.	Shore seine
	16–17/8/16	8	–	9.7	8–12	Bliss Island	Shore seine (Mavor, 1918)
	21/8/46	10	12	12.0	11–14	St. Andrews, N.B.	Unknown
	17/8/61	65	12	11.3	8–15	St. Andrews, N.B.	Lift net
	13/9/61	76	12	12.2	10–17	St. Andrews, N.B.	Lift net
	18/10/61	146	–	15.0	11–20	St. Andrews, N.B.	Lift net
	19/10/30	3	–	14.0	13–16.5	Sandy Cove, N.S.	Unknown
I	6/6/47	18	–	22.0	20–25	St. Andrews, N.B.	Unknown
	14/6/60	6	–	18.8	17.4–19.5	Freeport, N.S.	Hook and line
	16/6/61	41	19	18.7	17–21	St. Andrews, N.B.	Lift net
	12/7/61	18	22	21.9	20–24	St. Andrews, N.B.	Lift net
	4/8/16	2	–	30.5[a]	29–32[a]	Campobello Is.	Shore seine (Mavor, 1918)
	8–9/8/60	20	–	21	18–23	St. Andrews, N.B.	Lift net, hook and line
	11/8/60	73	–	24	20–29	Campobello Is.	Hook and line
II	5/6/61	280	32	31	25–35	Pollock Shoal[b]	Otter trawl
	4/8/16	16	39	39.2	35–45	Campobello Is.	Shore seine (Mavor, 1918)
	3/8/16	57	39	39.6	30–47	Campobello Is.	Shore seine
	11/8/60	2	–	33.5	33–34	Campobello Is.	Hook and line

[a]Obviously incorrect determination of age.
[b]Offshore collection.

the Barents Sea (Mironova, 1961). The groups of small fry in the Bay of Fundy collections had an average length of 6.5 cm in June and lacked hyaline zones in their otoliths; these were evidently the 0-class of young pollock. The mean lengths of this group increased to 14–15 cm in October. A second group of juveniles had average sizes of 19–22 cm in June and 21–24 cm in early August. These had a single hyaline zone in their otoliths and were assumed to be 1 year old. Larger fish with 2 hyaline zones were only occasionally collected. The formation of successive hyaline zones in the otoliths is therefore correlated with the peaks in the size compositions of "harbour" pollock.

The mean lengths of the year-classes of Bay of Fundy fish are similar to those of western Norway (Fig. 19). The mean lengths of Faroese fish (Bertelsen, 1942) are slightly shorter and those of the Barents Sea are shorter still (Fig. 19). However, there appear to be only slight variations in the growth rates in the different regions, and it could be that these differences in mean lengths are due to differences in the spawning times.

Off western Norway and in the Barents Sea "harbour" pollock grow most rapidly in the summer (May–October) and only slowly, if at all, in the winter (November–April). The data are less complete for the Bay of Fundy but the same tendency may be present.

There are small variations in the mean lengths of "harbour" pollock in different localities. These have been ascribed by Mavor (1918) to movements of fish into deeper water as they grow larger, and to differences in the time of arrival at the shore by Bertelsen (1942). It is also evident that the availability of food can affect the growth rate, as suggested by Lie (1961). Fish collected in harbours in the Bay of Fundy invariably contained quantities of refuse, while those from the open coast contained only small crustacea and other organisms. The longer mean lengths of the fish caught in harbours (Table VI) could therefore be ascribed to better feeding conditions.

Offshore Pollock

The ages of the larger, offshore pollock were estimated by counting the number of hyaline zones from the nucleus out to the narrow tip in cross-sections of their otoliths. The zones could easily be distinguished in fish up to 8 years of age, but were difficult to recognize in the older fish.

The validity of the method was established for these larger fish by an analysis of the changes in appearance of the otolith edges. When counting the hyaline zones in the otolith the appearance of the edge of the otolith was recorded as being narrow hyaline, wide hyaline, narrow opaque or wide opaque. The frequencies of each of these classes for fish less than 8 years old in different months of the year are shown in Fig. 20. The Figure shows that the deposition of the hyaline zone begins in some fish in the autumn (October? and November) and is taking place in most fish in the winter (December? and January), whereas the opaque material appears in some fish as early as the winter (December?) and in practically all in the summer (May–September?). Thus in most fish there appear to be one hyaline and one opaque zone deposited on the otolith in each year, and there is justification for considering the number of hyaline zones in the

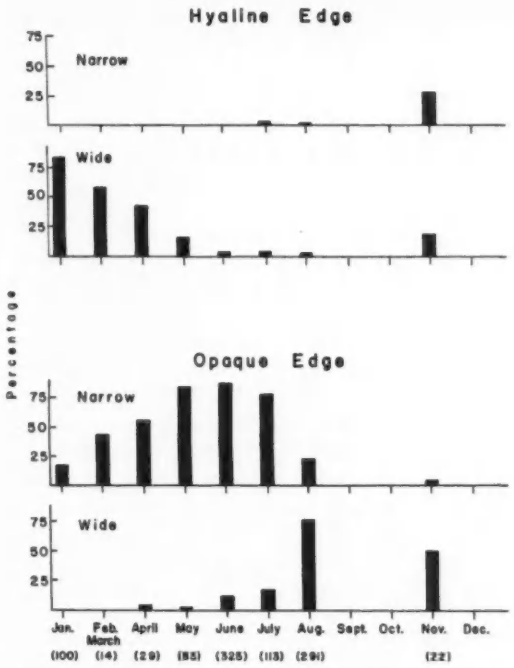


FIG. 20. Seasonal changes in otolith edges of fish less than 8 years old. Numbers of fish in parentheses.

otolith an indication of the age for fish less than 8 years old. A similar cycle is evident in the fish more than 7 years old but the turnover from one to the other appears to occur later. This may be due to differences in the yearly growth pattern, or, as seems more likely, to difficulty in determining the nature of the edge when the zones are narrow. In either case, it would have no effect on the age determinations, which can also be based on the number of hyaline zones.

Although the returns of tagged fish are too few to allow a detailed analysis of growth, the recorded increments are comparable to those determined from otoliths (Table VII). This further supports the otolith method of age determinations.

Preliminary analysis of age–length data showed that there is no noticeable difference between the growth rates of the males and females, and in the subsequent calculations the data for both sexes have been combined.

The mean lengths at each age of all Bay of Fundy samples of 1960 and 1961 are shown in Table VIII and plotted in Fig. 21. The curves fitted by Walford graphs (Ricker, 1958) show that growth is rapid in the early years, but slows down at about the age of 6 at the onset of sexual maturity. The mean lengths were noticeably greater in 1960 than in 1961, but the reason for this is unknown.

TABLE VII. Growth increments of tagged fish, 1960–61.

Months free:	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Age when released	Average increments in cm with numbers of fish in parentheses																	
yr																		
5½	1(1)	...	...	...	...	6(1)	5(1)	4(1)	5(1)	...	7(1)	...	...	9(1)	...	...	...	...
6½	1(1)	...	...	...	6(1)	...	...	...	...	4(1)	...	3(2)	...	...	...	...	...	...
7½	...	2(1)	...	2(2)	...	...	...	2(1)	...	...	...	...	...	...	...	...	...	...
8½	0(1)	...	...	...	...	...	2(1)	...	...	...	...	...	7(1)	...	...	...	...	6(1)
9½	...	...	...	0(1)	...	...	...	3(1)	...	1(1)	...	...	...	...	...	...	...	...
10½	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
11½	1(1)	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
12½	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...

The relative importance of the summer increment decreases as the fish grow older. The June–August increment of 1960 amounted to 67% of the year's (June–June) growth in 3-year-olds, 40% for the 4-year-olds and 17% for the 5-year-olds. This suggests that growth is most rapid in the summer months in the young fish (see also "harbour" pollock), but is less concentrated into one season of the year as the fish grow older. The summer growth occurs during the period that most of the fish are depositing opaque material on the otolith.

The June–August increments of 1961 were smaller than those of 1960, which means that growth in this year was less than in 1960.

The growth rate of pollock in the Campobello area was studied by Mavor (1918) and in the southern Gulf of Maine by Hoberman and Jensen (1962), with scales used for age determinations. Otoliths collected on the Scotian Shelf and samples supplied by the U. S. Fish and Wildlife Service from the southern Gulf of Maine have made possible studies of the pollock growth rates in these areas in the present investigation. The growth rates in various regions of the eastern Atlantic have been studied by Saemundsson (1929), Bertelsen (1942), Schmidt (1955, 1958, 1959), Fridriksson (1952, 1953, 1956, 1958) and Mironova (1961). The results of all these investigations are summarized in Table VIII.

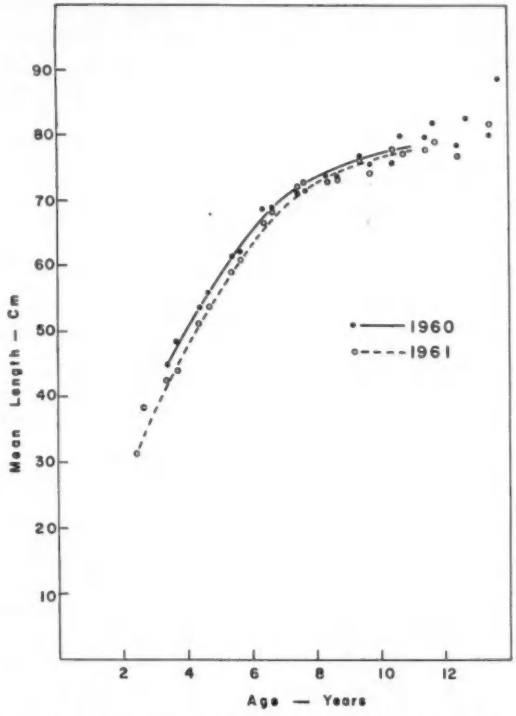


FIG. 21. Growth of pollock in the Bay of Fundy, 1960, 1961.

TABLE VIII. Mean lengths (M.L.) in cm of the age groups in various regions.

Location:	Laurentian Channel		Scotian Shelf				Bay of Fundy					Southern Gulf of Maine				Iceland						Faroes			Barents Sea
Authors:											Mavor (1918)	Hoberman and Jensen (1961)				Fridriksson (1953, 1958)		Saemundsson (1929)		Schmidt (1955, 1958)		Schmidt (1958)	Bertelsen (1942)		Mironova (1961)
Ageing material:	Otoliths		Otoliths		Otoliths		Otoliths				Scales	Otoliths		Scales		Otoliths		Scales		Otoliths		Otoliths		Scales	Otoliths
Year:	1961		1946		1961		Aug. 1960		Aug. 1961		1916	1961		1960		1952	1956	1923	1927–8	1954	1952–6	1956			
	No.	M.L.	No.	M.L.	No.	M.L.	No.	M.L.	No.	M.L.	M.L.	Mo.	M.L.	M.L.		M.L.	M.L.	M.L.	M.L.	M.L.	M.L.	M.L.		M.L.	M.L.
Age																North Coast				SW Coast					
½	...	...	...	...	...	...	302	11	65	11	...	...	...	...		...	...	...	...	...	...	...	...	...	...
1	...	...	...	...	...	...	...	...	...	...	...	...	...	19		...	...	...	...	...	...	...	...	...	...
1½	...	...	...	...	...	...	20	21	...	...	...	...	...	...		...	...	...	...	...	...	...	...	...	...
2	...	...	...	...	...	...	...	...	...	...	...	...	...	31		...	...	...	...	...	...	...	...	...	...
2½	...	...	...	...	...	...	...	...	10	38	...	...	...	...		36	36	...	...	...	...	...	35	31	...
3	21	38	...	...	9	37	...	...	...	...	...	...	...	41		...	...	...	...	...	...	...	...	...	...
3½	...	...	...	...	...	...	4	49	35	44	...	...	...	...		46	50	...	...	...	...	...	47	40	...
4	39	45	...	...	7	48	...	...	...	...	...	...	...	50		...	...	...	...	...	...	...	...	...	...
4½	...	...	...	...	...	...	10	56	70	54	64	9	52	...		55	57	...	...	...	...	...	58	50	...
5	6	54	...	...	2	53	...	...	...	...	...	...	...	57		...	...	...	...	...	57	...	...	...	...
5½	...	...	...	...	...	...	22	62	54	61	70	25	57	...		62	64	...	73	...	...	...	65	50	...
6	10	64	...	...	7	68	...	...	...	...	...	...	...	63		...	...	...	...	69	67	70	...	...	...
6½	...	...	...	...	...	...	10	69	38	69	75	15	67	...		74	70	...	79	...	...	...	75	72	...
7	10	70	3	75	19	73	...	...	...	...	...	...	...	68		...	...	...	...	77	76	77	...	...	...
7½	...	...	...	...	...	...	18	72	24	73	...	6	73	...		77	...	101	89	...	...	...	81	82	...
8	5	73	10	79	24	78	...	...	...	...	...	...	...	...		...	...	...	...	83	83	84	...	...	...
8½	...	...	...	...	...	...	24	74	19	74	...	7	73	...		...	...	106	93	...	...	...	87	88	...
9	6	77	25	81	30	79	...	...	...	...	...	...	...	...		...	...	...	...	91	89	89	...	...	...
9½	...	...	...	...	...	...	16	76	13	74	...	8	74	...		...	...	106	...	...	...	...	84	...	...
10	4	82	9	82	20	81	...	...	...	...	...	...	...	...		...	...	...	...	93	93	92	...	...	...
10½	...	...	...	...	...	...	7	80	14	77	...	6	79	...		...	...	...	...	...	...	...	91	...	...
11	...	...	11	84	5	82	...	...	...	...	...	...	...	...		...	...	...	...	98	96	95	...	...	...
11½	...	...	...	...	...	...	4	82	6	79	...	...	...	...		...	...	...	...	...	...	...	...	...	...
12	...	...	7	89	12	85	...	...	...	...	...	...	...	...		...	...	...	...	100	98	98	...	...	...
12½	...	...	...	...	...	...	...	...	...	...	...	...	...	...		...	...	...	...	...	...	...	...	...	...
13	...	...	4	87	4	88	...	...	...	...	...	...	...	...		...	...	...	...	100	100	101	...	...	...
13½	...	...	...	...	...	...	...	...	...	...	...	...	...	...		...	...	...	...	...	...	...	...	...	...
14	...	...	3	90	5	91	...	...	...	...	...	...	...	...		...	...	...	...	to 112 at 19	to 110 at 20	to 110 at 20			

The average lengths at each age when determined from scale readings are often greater than those derived from otolith readings. It is probable that the scale readings do not give a true measure of the ages of old fish because of the difficulty in distinguishing the outer rings; this is also the conclusion of Schmidt (1955).

The growth rate of pollock in the Bay of Fundy is similar to that of other groups for which otoliths have been used for age determination (Laurentian Channel, Scotian Shelf, southern Gulf of Maine, Iceland and Barents Sea) up to the age of 6 years; beyond this the Bay of Fundy pollock appear to grow more slowly than those of the Scotian Shelf or the eastern Atlantic. These differences may be real, or due to biased sampling of the Bay of Fundy fish.

Pollock catches in the Bay of Fundy are normally limited to a narrow size range of fish due to the segregation by size in pollock schools and because the schools are apparently characteristic of certain locations. Because segregation is according to size, each school contains fast-growing young fish and slow-growing old fish at the extremes of the size range. Thus the mean lengths at each age will vary with the size range of the school (Table IX) and will not give representative values for the entire population.

Since few fish over 80 cm in length were present in the Bay of Fundy samples, the apparent growth rate may have been underestimated at the older ages. On the Scotian Shelf and in the eastern Atlantic, where the apparent growth rate is not so depressed in the older fish, larger fish (up to 110 cm) are caught.

TABLE IX. Mean lengths of age groups in pollock schools with different size ranges, June 1961.

Size range (cm):	30–45		45–60		60–75		65–85	
Age	No.	Mean length	No.	M.L.	No.	M.L.	No.	M.L.
years		*cm*		*cm*		*cm*		*cm*
4	5	50.0	66	53.7	14	54.5	...	...
5	7	58.3	51	59.3	27	60.0	...	...
6	...	...	16	66.1	27	66.3	12	69.1

LENGTH–WEIGHT RELATIONSHIP

The weights in ounces of round pollock from the Scotian Shelf collected in April to May 1961, and of round and gutted-gilled pollock from the Bay of Fundy caught in June and August 1961 were determined with spring scales (Table X). In contrast to the findings of Craigie (1927), there was no noticeable difference between males and females, and the data were not analysed separately.

The regressions of log weight against log length for each sample are hown in Fig. 22. There is evidently an increase in both round and gutted-gilled weights from April–May to August. This occurs when opaque material is being deposited on the otoliths and the mature fish are in the recovering and ripening phases of the reproductive cycle.

TABLE X. Weight–length relationship of round and gutted-gilled pollock, 1961.

Length	Scotian Shelf[a] April–May 1961 Round		Bay of Fundy[b] June 1961 Round		Bay of Fundy[c] August 1961 Round		Bay of Fundy[d] June 1961 Gutted-gilled		Bay of Fundy[e] August 1961 Gutted-gilled	
	No. fish	Mean weight	No. fish	Mean weight	No. fish	Mean weight	No. fish	Mean weight	No. fish	Mean weight
cm		*oz*		*oz*		*oz*		*oz*		*oz*
30	...	...	2	10.5	...	...	2	9	...	...
31	...	...	2	12	...	...	2	10	...	...
32	...	...	4	12.3	...	...	4	10.2	...	...
33	...	...	2	14	1	15	2	12.5	1	13
34	...	...	1	18	...	...	1	14	...	...
35	...	...	2	17	...	...	2	14.5	...	...
36	1	16	1	18	2	20.5	1	16	2	17.5
37	...	...	...	...	...	...	...	...	...	...
38	...	...	1	19	1	27	1	16	1	21
39	1	20	2	23	2	25	2	19	2	20.5
40	...	...	2	31	2	30.5	1	20	2	24.5
41	...	...	...	...	3	32.3	...	...	2	26
42	...	...	1	31	...	...	1	26	1	28
43	...	...	2	34.5	3	36.3	2	25	4	32.8
44	...	...	3	35.7	2	43	3	29	1	34
45	...	...	4	40.5	3	44.3	6	27	3	35.7
46	1	32	2	44	3	47.6	...	...	3	38.7
47	...	...	3	46	2	52	3	36.3	2	40.5
48	1	36	2	52	4	52.2	1	40	5	44.8
49	...	...	3	52	7	56.7	2	40	7	47.4
50	...	...	3	55.2	10	59.8	4	44.8	9	50.1
51	...	...	3	56	4	67.5	2	46	6	54
52	1	48	4	60.5	2	72.5	4	49.5	1	56
53	...	...	6	65.2	4	71	7	54	7	57.7
54	2	62	4	64	...	...	4	56.2	3	62.7
55	...	...	5	69.3	13	77.1	4	60	13	64.7
56	...	...	2	72	4	78	4	59	7	67.4
57	...	...	4	71.3	5	84	6	60	7	70.9
58	...	...	6	80.6	2	92	7	64	6	74
59	...	...	7	85.1	7	97.7	7	70	7	79.3
60	...	...	3	86	2	102	2	68	3	82.7
61	...	...	3	91	5	100.8	6	73	5	81.6
62	1	96	5	93	5	107.2	3	75.7	10	87.1
63	...	...	3	99.7	1	108	2	82	4	88
64	...	...	3	102.3	5	112.5	3	87	5	96
65	1	92	4	107	5	124	6	91.5	5	99.2
66	1	108	3	114	4	128	3	94.7	4	104.5
67	1	112	4	110	4	128	5	93	5	104.8
68	1	104	2	110	4	133	3	101	2	106
69	2	102	6	113	3	142.7	5	102.2	10	121.4
70	1	116	5	129.6	4	145	3	113	4	127
71	7	124	4	136.5	5	148.8	3	118.7	9	132
72	2	126	5	136.4	4	152	6	112.7	12	131
73	3	146	6	141.3	2	150	6	117	10	135.8
74	4	146	3	141.3	6	164.7	3	119.3	11	139
75	6	150	7	155.4	4	174.5	8	132.7	6	144
76	3	145	4	157	3	176	2	134	8	150
77	9	168	3	169.3	3	183.3	4	138.2	10	155.1
78	7	167	3	172	5	183.6	8	145.2	3	154.7
79	8	170	3	177.6	6	188.7	3	147	6	151.5
80	6	178	1	164	6	199.7	...	...	7	170.3
81	12	177	2	186	1	191	2	157.5	...	...
82	6	195	4	187.5	1	220	4	158	1	168
83	7	199	...	...	1	204	...	...	...	...
84	4	192	...	...	1	246	...	...	...	...

TABLE X. (continued)

Length	Scotian Shelf[a] April–May 1961 Round No. fish	Scotian Shelf[a] April–May 1961 Round Mean weight	Bay of Fundy[b] June 1961 Round No. fish	Bay of Fundy[b] June 1961 Round Mean weight	Bay of Fundy[c] August 1961 Round No. fish	Bay of Fundy[c] August 1961 Round Mean weight	Bay of Fundy[d] June 1961 Gutted-gilled No. fish	Bay of Fundy[d] June 1961 Gutted-gilled Mean weight	Bay of Fundy[e] August 1961 Gutted-gilled No. fish	Bay of Fundy[e] August 1961 Gutted-gilled Mean weight
cm		*oz*		*oz*		*oz*		*oz*		*oz*
85	3	205	...	...	...	...	1	190	...	...
86	3	217	...	...	...	...	...	...	...	...
87	3	228	...	...	...	...	...	...	...	...
88	...	...	1	240	...	...	...	...	...	...
89	2	252	...	...	...	...	...	...	...	...
90	...	...	...	...	...	...	...	...	...	...
91	2	268	...	...	...	...	...	...	...	...
92	2	275	...	...	...	...	...	...	...	...
93	...	...	...	...	...	...	...	...	...	...
94	...	...	...	...	...	...	...	...	...	...
95	...	...	...	...	...	...	...	...	...	...
96	1	302	1	296	...	...	...	...	...	...
N	125		179		176		171		222	

[a]Log $y = \bar{4}.6526 + 2.94 \log x$.
[b]Log $y = \bar{4}.9060 + 2.82 \log x$.
[c]Log $y = \bar{4}.7269 + 2.95 \log x$.
[d]Log $y = \bar{4}.4950 + 3.01 \log x$.
[e]Log $y = \bar{4}.6144 + 2.97 \log x$.

SIZE AND AGE AT MATURITY

The sex and maturity were determined by visual examination of the gonads. The categories and criteria used to distinguish them were similar to those employed by Powles (1958) for *Gadus morhua*. Since most of the fish were caught from May to June when they were in the recovering phase of the reproductive cycle, it was often difficult to determine whether small fish were immature or recovering.

The curves of size at maturity, fitted by probit analysis (Fleming, 1960), are shown in Fig. 23 and the ages at maturity in Table XI. The males mature when 4–7 years old and 50–65 cm in length (50% mature at 58 cm). The females mature at a slightly older age (5–7 years old) and larger size (55–70 cm; 50% mature at 62.5 cm). These observations are in agreement with those of European investigators who have found that almost all pollock are mature by the age of 6 (Bertelsen, 1942; Mironova, 1961; Schmidt, 1955).

REPRODUCTIVE CYCLE

The percentages of pollock in the different phases of the reproductive cycle in different months are given in Fig. 24. This shows that spawning occurs in the winter and is largely finished by February to March off Nova Scotia. This agrees with the spawning season in the southern Gulf of Maine but is earlier than that of the eastern Atlantic where it takes place from February to May off Norway (Bertelsen, 1942), and from January to April in the North Sea (Baranenkova,

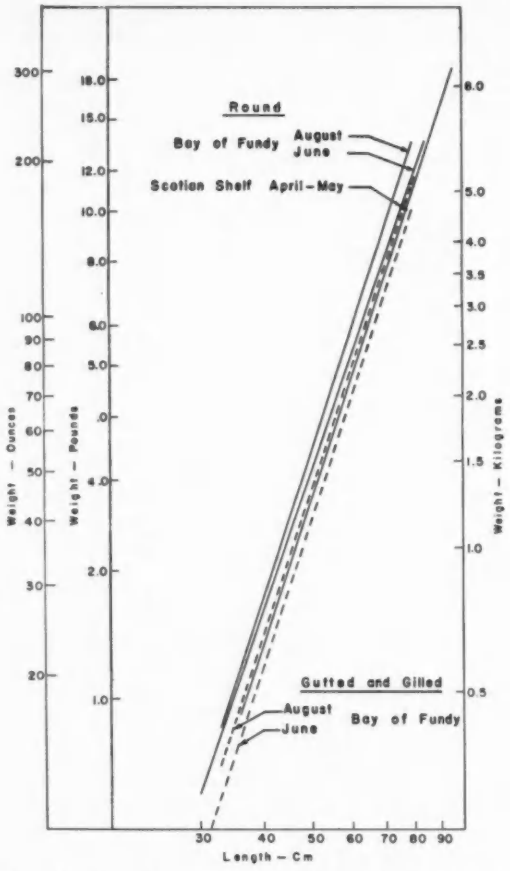


FIG. 22. Length–weight relationships of round and gutted-gilled pollock, 1961.

TABLE XI. Age at maturity of pollock in the Bay of Fundy, 1960–61.

Age	Males		Females	
	No.	Mature	No.	Mature
		%		%
3	48	0	36	0
4	99	13	107	1
5	99	73	101	45
6	57	95	60	92
7	50	98	39	97

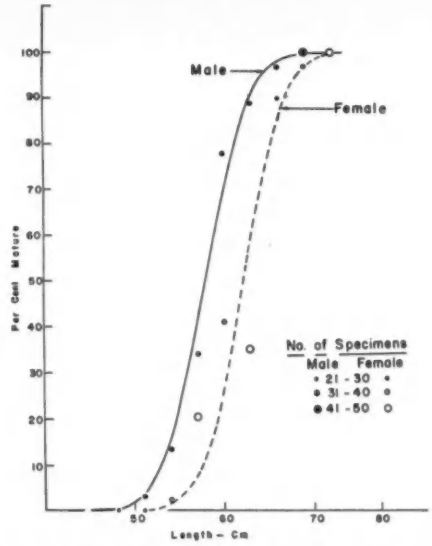


FIG. 23. Size at maturity of male and female pollock in the Bay of Fundy, 1960, 1961.

1957). During May and June all specimens examined in the Bay of Fundy were in the "recovering" phase. In July a few ripening males were observed. By August most of the males were ripening and the first ripening females were recorded. Whether this difference in the timing of the reproductive cycles of the males and females has any effect on their behaviour or distribution is unknown.

FOOD

The stomach contents of 1052 Bay of Fundy pollock were examined in the field and the volume and composition recorded. Fifty of these were examined in detail in the laboratory to check on the estimated volumes and to identify food items. The results of the field examination of 344 stomachs from the Scotian Shelf and Laurentian Channel were also analysed. The results of these analyses, arranged in 6 size categories, are given in Tables XII and XIII and Fig. 25. The field observations of the offshore pollock agree closely with the laboratory analyses and are used as the basis of the subsequent discussion, but for the "harbour" pollock only the laboratory analyses could be used as the difference between the field observations and laboratory analyses were large, due to the small volume of the stomach contents and the small size of the food items.

"HARBOUR" POLLOCK

Most of the "harbour" pollock were caught in this investigation with a baited lift-net and many contained bait. Their "normal" diet is assumed to be the other food found in the stomachs at the same time.

TABLE XII. Stomach content analysis, Bay of Fundy, May–August 1960, 1961.

	"Harbour" pollock						Offshore pollock											
	8–15 cm (age 0)			17–26 cm (age I)			27–40 cm			41–60 cm			61–74 cm			75+ cm		
	F[a]	L[b]	Vol.	F	L	Vol.	F	L	Vol.	F	L	Vol.	F	L	Vol.	F	L	Vol.
	no.	*no.*	%	*no.*	*no.*	%	*no.*	*no.*	%	*no.*	*no.*	%	*no.*	*no.*	%	*no.*	*no.*	%
No. examined	39	16		56	14		19	2		380	6		389	7		169	5	
Contents everted										2			5			9		
Empty	2			2						5			15			7		
No. with food	37	16		54	14		19	2		373	6		369	7		153	5	
Bait	14			39	2													
No. with other food	26	16		24	14		19	2		373	6		699	7		153	5	
Crustacea	22	16	84	18	14	94	19	2	98	364	6	95	356	7	93	141	5	83
Decapoda	2	1	0	10	6	26	0	0	0	2	0	<1	2	0	<1	0	0	0
Crago septemspinosus	1	0		10	6													
Zoea	1	1		0	0													
Euphausiacea	0	0	0	6	5	20	14	2	90	317	4	92	347	5	92	140	5	83
Meganyctiphanes norvegica					4			1			4			4			5	
Thysanoessa inermis					1			1			1			2			2	
Thysanoessa raschii											1			1				
Thysanoessa longicaudata														1				
Amphipoda	15	12	74	10	13	37	0	1	0	59	3	2	36	4	1	6	2	<1
Gammaridea		6	27		9	27		1			3			2			1	
Orchomenella minuta					3													
Anonyx sp.					1													
Ampelisca aequicornis?					2													
Metopa alderi											2							
Monoculodes intermedius								1			1			2				
Parapleustes assimilis								1										
Calliopius laeviusculus					3													
Pontogeneia inermis					3													
Gammarus oceanicus		2			2													
Gammarus lawrencianus					1													
Marinogammarus obtusatus					1													
Hyale nilssoni					1													
Orchestia platensis		1																
Leptocheirus pinguis		1			2												1	

TABLE XII. (continued)

	"Harbour" pollock						Offshore pollock											
	8–15 cm (age 0)			17–26 cm (age I)			27–40 cm			41–60 cm			61–74 cm			75+ cm		
	F[a]	L[b]	Vol.	F	L	Vol.	F	L	Vol.	F	L	Vol.	F	L	Vol.	F	L	Vol.
	no.	*no.*	%	*no.*	*no.*	%	*no.*	*no.*	%	*no.*	*no.*	%	*no.*	*no.*	%	*no.*	*no.*	%
Amphipoda, Gammaridea (continued)																		
Corophium sp.		1			1													
Ericthonius hunteri		2			1													
Ischyrocerus anguipes		1									2			1				
Dulichia porrecta											1							
Dulichia sp.											1							
Caprellidea		9	43		1	10					2							
Aeginella longicornis		7									1							
Caprella septentrionalis		8									2							
Caprella linearis		2									1							
Caprella acutifrons		1									1							
Hyperiidea		2	4		2						2			4				
Themisto gaudichaudi		1									2			4			2	
Themisto abyssorum														1			2	
Hyperia galba		1			2													
Hyperoche medusarum														2				
Isopoda	0	1	<1	1	1	<1	0	0	0	0	0	0	0	0	0	0	0	0
Jaera marina		1																
Limnoria lignorum					1													
Cumacea	0	0	0	1	1	<1	0	0	0	0	0	0	0	0	0	0	0	0
Diastylis sp.					1													
Pseudocuma sp.					1													
Copepoda	4	7	10	5	4	11	10	2	8	70	5	1	4	5	<1	0	2	0
Calanoida		3	6		4	11	10	2	8	70	5	1	4	5	1	0	2	0
Calanus finmarchicus		3	6		4	11		2			5			1			0	
Calanus hyperboreus								2			4			2			0	
Euchaeta norvegica								2			4			5			2	
Harpacticoida		4	4		0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostracoda	0	0	0	1	1	<1	0	0	0	0	0	0	0	0	0	0	0	0
Insecta	4	6	7	0	1	<1	0	0	0	0	0	0	0	0	0	0	0	0
Chaetognatha	0	0	0	1	1	<1	0	0	0	2	0	<1	5	3	<1	0	0	0

TABLE XII. (continued)

	"Harbour" pollock						Offshore pollock											
	8–15 cm (age 0)			17–26 cm (age I)			27–40 cm			41–60 cm			61–74 cm			75+ cm		
	F[a]	L[b]	Vol.	F	L	Vol.	F	L	Vol.	F	L	Vol.	F	L	Vol.	F	L	Vol.
	no.	*no.*	%	*no.*	*no.*	%	*no.*	*no.*	%	*no.*	*no.*	%	*no.*	*no.*	%	*no.*	*no.*	%
Annelida	0	2	<1	0	0		1	1	<1	5	2	<1	2	5	<1	1	1	<1
Tomopteris sp.		0					1	1		5	2		2	5		1	1	
Others		2																
Coelenterata & Ctenophora	0	1	<1	0	0	0	0	0	0	52	2	<1	33	0	3	10	1	1
Medusae & Ctenophores	0	0	0	0	0	0	0	0	0	52	2	<1	33	0	3	10	1	1
Hydroids	0	1	1	0	0	0	0	0	0	0	1	<1	0	0	0	0	0	0
Mollusca	0	0	0	0	0	0	0	0	0	2	2	<1	2	1	<1	1	0	<1
Pteropoda	0	0	0	0	0	0	0	0	0	0	0	0	2	1	<1	0	0	0
Clione limacina													2	1				
Decapoda	0	0	0	0	0	0	0	0	0	1	2	<1	0	0	0	1	0	<1
Gasteropoda	0	0	0	0	0	0	0	0	0	1	0	<1	0	0	0	0	0	0
Pisces	0	2	7	8	2	3	5	0	2	69	2	2	34	4	3	29	1	16
Ammodytes americanus	0			0	0		5	0		35	1		7	2		1	0	
Maurolicus pennanti	0	0		0	0		0	0		5	0		3	0		0	0	
Menidia menidia	0	2		8	2		0	0		0	0		0	0		0	0	
Clupea harengus	0	0		0	0		0	0		0	0		4	0		9	0	
Clupea harengus — larvae	0	0		0	0		0	0		1	1		0	0		0	0	
Anarhichas lupus — juveniles	0	0		0	0		0	0		8			2			0	0	
Urophycis sp.	0	0		0	0		0	0		0			1	0		1	0	
Merluccius bilinearis	0	0		0	0		0	0		0	0		0	0		1	0	
Hippoglossoides platessoides	0	0		0	0		0	0		0	0		0	0		2	0	
Unid. larvae	0	0		0	0		0	0		1	0		1	0		0	0	
Unidentifiable material	2	2	<1	0	0	0	0	0	0	2	0	<1	2	0	<1	0	0	<1

[a]Field observations.

[b]Laboratory analyses.

TABLE XIII. Stomach content analysis, Scotian Shelf and Laurentian Channel, 1959, 1961.

	Scotian Shelf, July 1959						Scotian Shelf, April-May 1961								Laurentian Channel, January 1961							
	41–60 cm		61–74 cm		75+ cm		27–40 cm		41–60 cm		61–74 cm		75+ cm		27–40 cm		41–60 cm		61–74 cm		75+ cm	
	Vol.		Vol.		Vol.		Vol.		Vol.		Vol.		Vol.		Vol.		Vol.		Vol.		Vol.	
	no.	%	*no.*	%	*no.*	%	*no.*	%	*no.*	%	*no.*	%	*no.*	%	*no.*	%	*no.*	%	*no.*	%	*no.*	%
No. examined	9		41		11		9		11		35		121		16		55		20		16	
Everted	0		0		0		0												2			
Empty	0		0		0		4		5		21		65		1		6		6		3	
No. with food	9		41		11		5		6		14		56		15		49		14		13	
Crustacea	9	46	37	8	8	3	5	100	5	83	6	8	14	3	11	55	23	20	10	25	2	9
Euphausiacea	7	34	25	4	5	2	5	100	5	83	2	4	13	3	11	55	23	20	10	25	2	9
Amphipoda	6	12	25	4	3	1	0	0	0	0	4	4	1	<1	0	0	0	0	0	0	0	0
Decapoda	0	0	2	<1	0	0	0	0	0	0	0	0	1	<1	0	0	0	0	0	0	0	0
Mollusca	0	0	2	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	13	0	0
Pteropoda	0	0	2	<1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0
Decapoda	0	0	1	<1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Annelida	0	0	0	0	0	0	0	0	0	0	0	0	2	<1	0	0	0	0	0	0	0	0
Ctenophora and Medusa	2	1	14	2	2	1	0	0	0	0	1	<1	8	2	0	0	0	0	0	0	0	0
Pisces	2	53	5	89	3	96	0	0	1	17	9	92	38	94	6	45	33	80	9	62	12	91
Merluccius bilinearis	0	0	2	89	3	96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ammodytes americanus	2	53	1	<1	1	<1	0	0	1	17	5	81	22	86	0	0	0	0	0	0	0	0
Mallotus villosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	5	0	0
Sebastes sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0
Gadus morhua	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0
Myctophum affine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	32	21	62	1	2	1	2

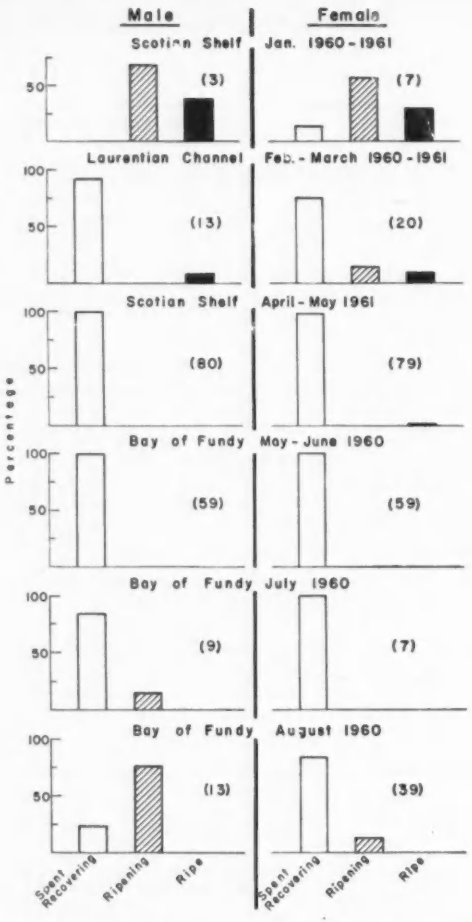


FIG. 24. Maturity stages of pollock from January to August, 1960, 1961 (numbers of fish in parentheses).

The pelagic post-larvae feed on small copepods (Marak, 1960). After moving into the shallow, sublittoral zone, these 0-class pollock feed mainly on small crustacea, particularly algae-inhabiting amphipods (*Gammarus*, *Orchestia*, *Corophium*, *Ericthonius*, *Ischyrocerus* and caprellids). Harpacticoid copepods and insects also occur in some stomachs but are of little importance by volume. The occurrence of intertidal *Gammarus* spp. and *Orchestia* suggests that these small fish may move into the intertidal zone when the tide rises. This was confirmed by direct observation on the beach near the Biological Station. Pelagic organisms such as calanoid copepods were of little importance in the diet. These observations are similar to those made by most European investigators (Bertelsen,

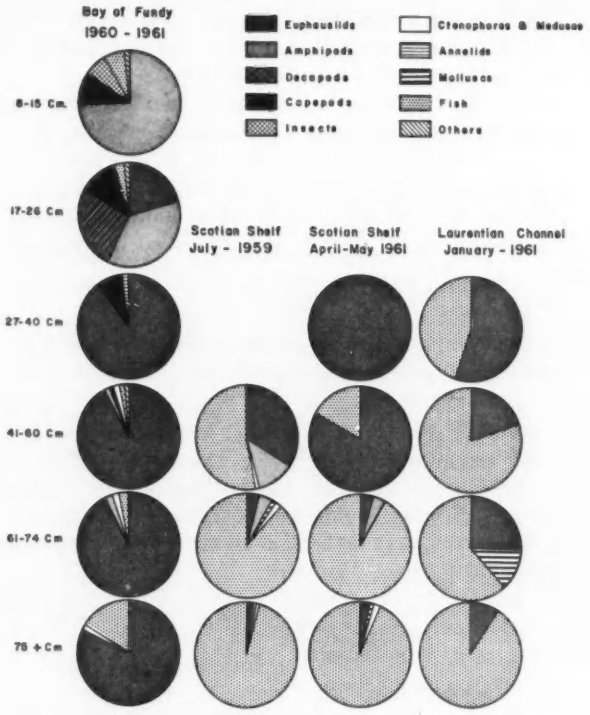


FIG. 25. Stomach contents, volume analysis, Bay of Fundy, Scotian Shelf and Laurentian Channel, 1959, 1960, 1961 (see Tables XII and XIII).

1942; Mironova, 1957, 1961; Lie, 1961). This diet may explain the scarcity of 0-class pollock on sandy and muddy shores where small crustacea are less abundant (personal observation; Wollebaek, 1900; Baranenkova, 1957). However, both Nordgaard (1902) and Lie (1961) reported 0-class pollock at southern Norway feeding chiefly on plankton and to a lesser extent on sublittoral and littoral seaweed-inhabiting crustacea.

The diet of the 1-year-old pollock is similar to that of the 0-class in the summer, except that plankton organisms (calanoid copepods, euphausiids and small fish) and the sand shrimp (*Crago septemspinosus*) are of more importance. Benthic organisms (algae-inhabiting amphipods and harpacticoids plus the sand shrimp) are less important than they are in the younger fish. This agrees with the observations of Mironova (1957, 1961).

OFFSHORE POLLOCK

The offshore pollock in the Bay of Fundy are predominantly plankton eaters, with euphausiids and particularly *Meganyctiphanes norvegica* the most important organism for all sizes. However, the data for the 27- to 40-cm fish may not be

representative of this size range since only a small number were examined. Smaller pollock (27–40 and 41–60 cm) consume calanoid copepods and the larger ones (75+ cm) eat fish in addition to the euphausiids.

On the Scotian Shelf and in the Laurentian Channel fish were more important than euphausiids in the food except at small sizes (27–40 cm). The differences in diet between areas cannot be based entirely on availability, as herring of various sizes are abundant at the mouth of the Bay of Fundy.

Offshore pollock were also reported as feeding mainly on pelagic euphausiids and fish in the eastern Atlantic by Wagner (1959) and Mironova (1961).

SUMMARY

1. The pollock is an amphiboreal Atlantic species whose largest landings in the western Atlantic are made at the mouth of the Bay of Fundy (ICNAF Division 4X).
2. The best catches of fish of commercial size are made at temperatures above 1.1°C, at depths of 20–100 fathoms (35–185 m), on the edges of shoals and banks where an abundant food supply is available. In Division 4X, where tidal turbulence keeps the summer surface temperature low and displaces the food, they may be caught at times in large numbers at the surface and in the shallow, sublittoral zone.
3. Spawning takes place in the southern Gulf of Maine and probably also on the Scotian Shelf, but not in the northern Gulf of Maine. The Bay of Fundy pollock are recruited from spawning in the southern Gulf of Maine and possible spawning on the Scotian Shelf.
4. The summer concentration of pollock in the Bay of Fundy appears to be a distinct group of fish from those found in the southern Gulf of Maine and south of western Nova Scotia. However, in the winter the Bay of Fundy pollock migrate south and spawn in the southern Gulf of Maine and possibly on the Scotian Shelf, presumably mixing with the fish in those areas at that time.
5. The juvenile pollock move inshore in the early summer. The first winter is apparently spent offshore, but the 1-year-old fish return to the shallow, sublittoral zone in the following summer. They disappear from the shallow, sublittoral zone in early August when 20–25 cm in length, and presumably move away from shore. The 2-year-old pollock may be found in deeper water near shore or on offshore banks, but their typical habitat is not known.
6. The offshore pollock show a marked gradient in their size compositions across the Bay of Fundy, with large fish (65–85 cm) found on the New Brunswick side, medium-size fish (60–75 cm) around Grand Manan and the smallest fish (45–60 cm) off western Nova Scotia.
7. Size segregation also occurs in catches from local areas and shows that schooling is an important feature of pollock behaviour.
8. The growth rate of the inshore "harbour" pollock is similar to that found in pollock caught off western Norway, but more rapid than that of Faroese and Barents Sea fish.

9. The growth rate of the larger offshore pollock is rapid until the fish are approximately 6 years old, but is much slower thereafter. The growth rate of the Bay of Fundy pollock is similar to that recorded for other areas, except at the older ages. It is suggested that this discrepancy may be caused by a failure to collect adequate samples of old fish in the Bay of Fundy, due to the segregation by size.
10. Both the round and the gutted-gilled weights of equal-sized pollock increased from April–May to August.
11. Male pollock were found to mature at ages of 4–7 and a size range of 50–60 cm. Females reach maturity when 5–7 years old and sizes of 55–70 cm.
12. Spawning occurs in the winter. In May and June all of the Bay of Fundy pollock examined were in the recovering phase of their reproductive cycle. In July a few ripening males were found. In August most males were ripening and a few ripening females were also observed.
13. The 0-class pollock were found to contain mainly algae-inhabiting organisms (amphipods, insects, harpacticoid copepods) in the summer. Planktonic organisms were of less importance. The 1-year-old fish had a similar but more restricted diet and consumed more plankton (euphausiids and calanoid copepods).
14. The offshore pollock in the Bay of Fundy are mainly plankton eaters and the euphausiid *Meganyctiphanes norvegica* is by far the most important organism. The smaller, offshore pollock also eat quantities of planktonic copepods and the largest sizes consume relatively more fish. On the Scotian Shelf and in the Laurentian Channel pollock were found to contain large quantities of fish, even at the smaller sizes.

ACKNOWLEDGMENTS

It is with pleasure that I acknowledge the help and suggestions given to me in the course of this investigation by Dr W. R. Martin and the staff of the groundfish investigation at the Fisheries Research Board of Canada Biological Station, St. Andrews, N.B. In particular, I would like to thank N. J. McFarlane and R. K. Robicheau for assistance in the field work of 1960 and 1961.

I would also like to thank A. M. Fleming of the Biological Station, St. John's, Newfoundland, and J. Bergeron of the Station de Biologie Marine, Grande-Rivière, P.Q., for information concerning the distribution of pollock off Newfoundland and in the Gulf of St. Lawrence, respectively; R. R. Marak and J. B. Colton, Jr., of the U.S. Fish and Wildlife Service, for information on the distribution of pollock larvae in the Gulf of Maine; the Biological Laboratory of the U.S. Fish and Wildlife Service, Woods Hole, Mass., for otoliths of pollock from the southern Gulf of Maine.

In addition, I would like to thank the captains, R. Green and L. Guptill, Jr., and crews of the commercial draggers *Sea Belle* and *Roxinda Ann* for their co-operation and help on cruises in the Bay of Fundy.

REFERENCES

BARANENKOVA, A. S. 1957. Raspredelenie i rost lichinok i malkov saidy (*Pollachius virens* (L.)). [Distribution and growth of the larvae and fry of the saithe (*Pollachius virens* L.).] *Trudy PINRO*, No. 10, pp. 145–160. [Translation from Fisheries Laboratory, Lowestoft, England.]

BATTLE, H. I. 1930. Spawning periodicity and embryonic death rate of *Enchelyopus cimbrius* (L.) in Passamaquoddy Bay. *Contrib. Canadian Biol. Fish.*, N.S. **5**(11): 361–380.

BERTELSEN, E. 1942. Contributions to the biology of the coalfish (*Gadus virens* L.) in Faroe waters with special regard to the youngest age groups. *Medd. Komm. Danmarks Fiskeri- og Havunders., Fiskeri*, **11**(2): 1–68.

BIGELOW, H. B. 1928. Physical oceanography of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, **40**: 511–1027. (Document No. 969).

BIGELOW, H. B., AND W. C. SCHROEDER. 1953. Fishes of the Gulf of Maine (First Revision). *U.S. Fish and Wildlife Serv., Fish. Bull.*, **53**: 1–577. (Fish. Bull. No. 74).

BOUSFIELD, E. L., AND A. H. LEIM. 1959. The fauna of Minas Basin and Minas Channel. *Bull. National Museum of Canada*, No. 166, 30 pp.

BUMPUS, D. F. 1960. Sources of water contributed to the Bay of Fundy by surface circulation. *J. Fish. Res. Bd. Canada*, **17**(2): 181–197.

CANADA DEPARTMENT OF MINES AND TECHNICAL SURVEYS, GEOGRAPHICAL BRANCH, OTTAWA. 1957. Atlas of Canada, East Coast Fisheries, Plate No. 59.

CANADA DEPARTMENT OF TRADE AND COMMERCE, DOMINION BUREAU OF STATISTICS. 1958. Fishery statistics of Canada, 1956.

1960. Fishery statistics of Canada, 1957.

COLES, R. J. 1926. Notes on Cape Lookout (North Carolina) fishes—1925. *Copeia* for 1926, **151**: 105–106.

COLTON, J. B., JR., AND R. F. TEMPLE. 1961. The enigma of Georges Bank spawning. *Limnol.* and *Oceanogr.*, **6**(3): 280–291.

CORNISH, G. A. 1912. Notes on fishes of Tignish, Prince Edward Island. *Contrib. Canadian Biol.*, 1906–1910, pp. 79–81.

CRAIGIE, E. H. 1927. Notes on the total weights of the squirrel hake, the pollock, the winter flounder, and the smelt, and on the weights of the liver and gonads in the hake and in the pollock. *Trans. Roy. Soc. Canada*, Ser. 3, Sect. V, **21**: 153–173.

DAY, C. G. 1958. Surface circulation in the Gulf of Maine as deduced from drift bottles. *U.S. Fish and Wildlife Serv., Fish. Bull.*, **58**: 443–473. (Fish. Bull. No. 141).

FISH, C. J. 1928. Production and distribution of cod eggs in Massachusetts Bay in 1924 and 1925. *Bull. U.S. Bur. Fish.*, **43**: 253–296. (Document No. 1032).

1936a. The biology of *Calanus finmarchicus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull.*, **70**: 118–141.

1936b. The biology of *Pseudocalanus minutus* in the Gulf of Maine and Bay of Fundy. *Ibid.*, **70**: 193–216.

1936c. The biology of *Oithona similis* in the Gulf of Maine and the Bay of Fundy. *Ibid.*, **71**: 168–187.

FLEMING, A. M. 1960. Age, growth and sexual maturity of cod (*Gadus morhua* L.) in the Newfoundland area, 1947–1950. *J. Fish. Res. Bd. Canada*, **17**(6): 775–809.

FRIDRIKSSON, A. 1952. Saithe. Remarks on the young saithe (*Gadus virens*, Linné) off the north coast of Iceland in 1950–1951. *Ann. Biol.*, Vol. 8 for 1951, pp. 42–44.

1953. Saithe. Remarks on the young saithe (*Gadus virens*, Linné) off the north coast of Iceland. *Ibid.*, Vol. 9 for 1952, pp. 43–45.

1954. Saithe. Occurrence of young saithe off the north coast of Iceland. *Ibid.*, Vol. 10 for 1953, pp. 42–43.

1956. Saithe. Icelandic stock. *Ibid.*, Vol. 11 for 1954, pp. 103–104.

1958. Saithe. Iceland stock. Remarks on the young saithe off the north coast of Iceland in 1956. *Ibid.*, Vol. 13 for 1956, pp. 156–157.

HILDEBRAND, S. F., AND W. C. SCHROEDER. 1928. Fishes of Chesapeake Bay. *Bull. U.S. Bur. Fish.*, **43**: 1–366. (Document No. 1024).

HOBERMAN, J. M., AND A. C. JENSEN. 1962. The growth rate of New England pollock. *Trans. Am. Fish. Soc.*, **91**: 227–228.

HUNTSMAN, A. G. 1918a. The effect of the tide on the distribution of the fishes of the Canadian Atlantic coast. *Trans. Roy. Soc. Canada*, Ser. 3, Sect. IV, **12**: 61–67.

1918b. Histories of new food fishes. I. The Canadian plaice. *Bull. Biol. Bd. Canada*, No. 1, 32 pp.

1923. Natural lobster breeding. *Ibid.*, No. 5, 11 pp.

1952. The production of life in the Bay of Fundy. *Trans. Roy. Soc. Canada*, Ser. 3, Sect. V, **46**: 15–38.

HUNTSMAN, A. G., AND M. E. REID. 1921. The success of reproduction in *Sagitta elegans* in the Bay of Fundy and the Gulf of St. Lawrence. *Trans. Roy. Canadian Inst.*, Vol. 13, Pt. 2, 14 pp.

INTERNATIONAL COMMISSION FOR THE NORTHWEST ATLANTIC FISHERIES. 1954–1961. *Statistical Bulletin* for the years 1952–1959, Vol. 2–9.

1961. Standing committee on research and statistics. Proceedings and selected reports 1961 annual meeting, pp. 46–47.

JENSEN, AD. S., AND P. M. HANSEN. 1931. Investigations on the Greenland cod (*Gadus callarias* L.) with an introduction on the history of the Greenland cod fisheries. *Rapp. Cons. Expl. Mer*, **72**: 1–41.

KENDALL, W. C. 1898. Notes on the food of four species of the cod family. *Rept. U.S. Fish. Comm.* for 1896, pp. 177–186.

LEGARÉ, J. E. H., AND D. C. MACLELLAN. 1960. A qualitative and quantitative study of the plankton of the Quoddy region in 1957 and 1958 with special reference to the food of the herring. *J. Fish. Res. Bd. Canada*, **17**(3): 409–448.

LIE, U. 1961. On the growth and food of 0-group coalfish, *Pollachius virens* (L.), in Norwegian waters. *Sarsia*, **3**: 1–36.

MARAK, R. R. 1960. Food habits of larval cod, haddock and coalfish in the Gulf of Maine and Georges Bank area. *J. Cons. Expl. Mer*, **25**(2): 147–157.

MARAK, R. R., AND J. B. COLTON, JR. 1961. Distribution of fish eggs and larvae, temperature, and salinity in the Georges Bank-Gulf of Maine area, 1953. *U.S. Fish and Wildlife Serv., Special Sci. Rept.—Fish.*, No. 398, 61 pp.

MARAK, R. R., J. B. COLTON, JR., AND D. B. FOSTER. 1962. Distribution of fish eggs and larvae, temperature, and salinity in the Georges Bank-Gulf of Maine area, 1955. *U.S. Fish and Wildlife Serv., Special Sci. Rept.—Fish.*, No. 411, 66 pp.

MARR, J. C. 1957. The problem of defining and recognizing subpopulations of fishes. *U.S. Fish and Wildlife Serv., Special Sci. Rept.—Fish.*, No. 208, pp. 1–6.

MARTIN, W. R. 1960. Predicted effects of proposed tidal power structures on groundfish catches in Charlotte County, N.B. *J. Fish. Res. Bd. Canada*, **17**(2): 169–173.

MAVOR, J. W. 1918. On the age and growth of the pollock in the Bay of Fundy. *Contrib. Canadian Biol.* for 1917–1918, pp. 111–125.

MIRONOVA, N. V. 1957. Biologia i promysel saidy. [Biology and fishing industry of pollock.] *Trudi Murmanskoi biologicheskoi stantsii* III, pp. 114–129. [Translation from Fisheries Laboratory, Lowestoft, England.]

1961. Biology of the Barents Sea saithe, *Pollachius virens* (L.). *Int. Revue ges. Hydrobiol.*, **46**(3): 447–459.

MCCRACKEN, F. D. 1960. Studies of haddock in the Passamaquoddy Bay region. *J. Fish. Res. Bd. Canada*, **17**(2): 175–180.

MCKENZIE, R. A. 1959. Marine and freshwater fishes of the Miramichi River and Estuary, New Brunswick. *J. Fish Res. Bd. Canada*, **16**(6): 807–833.

NEEDLER, A. W. H. 1937. Report on a biological study of fishery statistics of the Atlantic coast of Canada. *Biol. Bd. Canada, MS Rept. Biol. Sta.*, No. 97, 72 pp.

1940. A preliminary list of the fishes of Malpeque Bay. *Proc. Nova Scotian Inst. Sci.*, **20**(2): 33–41.

NORDGAARD, O. 1902. Oplysninger om seiens veks og aate. [In Norwegian, English summary]. *Bergens Museums Aarbog*, 1901(3): 1–21.

OLSEN, S. 1956. Saithe. Norwegian stock marking experiments. *Ann. Biol.*, Vol. 11 for 1954, pp. 104–105.

POWER, E. A. 1960. Fishery statistics of the United States, 1958. *U.S. Fish and Wildlife Serv., Statistical Digest* 49.

1961. Fishery statistics of the United States, 1959. *Ibid.*, 51.

POWLES, P. M. 1955. Studies of reproduction and feeding of Atlantic cod (*Gadus callarias* L.) in the southwestern Gulf of St. Lawrence. *J. Fish. Res. Bd. Canada*, **15**(6): 1383–1402.

REDFIELD, A. C. 1939. The history of a population of *Limacina retroversa* during its drift across the Gulf of Maine. *Biol. Bull.*, **76**: 26–47.

RICKER, W. E. 1958. Handbook of computations for biological statistics of fish populations. *Bull. Fish. Res. Bd. Canada*, No. 119, 300 pp.

ROJO, A. L. 1955. Datos sobre la edad del bacalao (*G. callarias* L.), eglefino (*Melanogrammus aeglefinus* L.), colin (*Pollachius virens* L.) y locha (*Urophycis tenuis* Mitch.) con indicación de las técnicas usadas. *Boletín del Inst. Español de Oceanografía*, No. 73, 16 pp.

1957. Length frequencies—pollock. *Int. Comm. NW Atlantic Fish., Sampling Yearbook*, **2**: 1–119.

SAEMUNDSSON, B. 1929. On the age and growth of the coalfish (*Gadus virens* L.), the Norway pout (*Gadus esmarki* Nilsson) and the poutassou (*Gadus poutassou* Risso) in Icelandic waters. *Medd. Komm. Danmarks Fiskeri- og Havunders., Fiskeri*, **8**(7): 1–37.

SANDSTRÖM, W. J. 1919. The hydrodynamics of Canadian Atlantic waters. *In* Canadian Fisheries Expedition, 1914–15, pp. 221–343. Department of the Naval Service, Ottawa.

SCHMIDT, J. 1905. The pelagic post-larval stages of the Atlantic species of *Gadus*. *Medd. Komm. Danmarks Fiskeri- og Havunders., Fiskeri*, **1**(4): 1–77.

1909. The distribution of the pelagic fry and the spawning regions of the Gadoids in the North Atlantic from Iceland to Spain. *Rapp. Cons. Expl. Mer*, **10**: 1–229.

SCHMIDT, U. 1955. Beiträge zur Biologie des Köhlers (*Gadus virens* L.) in den isländischen Gewässern. *Ber. Deutsch. Wiss. Komm. Meeresforsch.*, **14**(1): 46–82.

1958. Saithe. Iceland stock. German commercial landings. *Ann. Biol.*, Vol. 13 for 1956, pp. 157–160.

1959. Saithe. Iceland and Arcto-Norwegian stocks. German investigations on commercial saithe landings in 1957. *Ibid.*, Vol. 14 for 1957, pp. 136–143.

STEELE, D. H. 1958. Fishes taken in the Laurentian Channel, Gulf of St. Lawrence, between Bird Rocks and the Saguenay River, 1953 and 1954. *Fish. Res. Bd. Canada, MS Rept. (Biol.)*, No. 651, 32 pp.

THOMPSON, H. 1932. First list of fishes in the Newfoundland fishing area. *Rept. Newfoundland Fish. Res. Comm.*, **1**(4): 107–110.

TRITES, R. W., AND R. E. BANKS. 1958. Circulation on the Scotian Shelf as indicated by drift bottles. *J. Fish. Res. Bd. Canada*, **15**(1): 79–89.

VLADYKOV, V. D. MS, 1932. The pollock fishery of the Fundy area. MS on file at the Biological Station, St. Andrews, N.B., 116 pp.

VLADYKOV, V. D., AND D. E. MCALLISTER. 1961. Preliminary list of marine fishes of Quebec. *Naturaliste Canadien*, **88**(3): 53–78.

WAGNER, G. 1959. Untersuchungen über die Tagesperiodizität der Nahrungsaufnahme bei *Pollachius virens* L. *Kurze Mitt. Inst. Fischereibiol., Univ. Hamburg*, No. 9, pp. 61–103.

WOLLEBAEK, A. 1900. Some biological notes. *In* Fishing experiments in Norwegian fiords by J. Hjort and K. Dahl. *Rept. Norwegian Fish. and Marine Invest.*, **1**(1): 96–119.

Pycnogonida of the North American Arctic[1]

By Joel W. Hedgpeth

Pacific Marine Station
Dillon Beach, California

ABSTRACT

This report concerns 22 species of pycnogonids found between Point Barrow and the Baffin Bay–Davis Strait region, based on collections by the Calanus expeditions since 1947 and by G. E. MacGinitie at Point Barrow. One new species, from Point Barrow, is described. Three basic distribution patterns are recognized: a boreal, circumarctic or panarctic distribution, a high arctic and deeper boreal distribution related to the North Atlantic–Norwegian sea areas, and a Pacific boreal distribution. Neither of the latter two have circumpolar components. No relationship between arctic and antartic Pycnogonida can be demonstrated, and several arctic species carry their young until they are much more advanced than do antarctic species.

This report is based primarily on the material collected by the various Calanus expeditions in the Canadian arctic regions since 1947, and the collections made at Point Barrow in 1948–50 by George E. MacGinitie. This combined material constitutes the largest collection of pycnogonids so far made from these regions, which have been rather meagerly collected for pycnogonids in spite of the fact that two of the classic arctic species (and among the first pycnogonids to be adequately described) were collected in the Canadian archipelago during the arctic exploration craze of 120–140 years ago. There is a rich literature on arctic pycnogonids as a result of the studies of Scandinavian and Russian workers, but many significant zoogeographical and ecological problems remain unresolved because of the inadequate information from North American sector of the Arctic, as well as because of the lack of material from the deep arctic basins proper.

This is the third report on American arctic material. The first, by Cole (1921), was based on a single station of the Canadian Arctic Expedition, consisting of three species, and the confirmation of two records from Point Barrow. Some 22 years later Hedgpeth (1943) reported on material collected by several expeditions to Foxe Basin, Baffin Bay and west Greenland. In all, these papers listed thirteen species in this area. The present paper raises the known pycnogonid fauna from the region between Point Barrow to Baffin Bay to 22 species, of which one is apparently undescribed. Still another species probably belongs to the area but is not represented in the collections.

Records for two other species from near southern Greenland taken by the Vema expeditions are included in this report.

The collections by George E. MacGinitie were made while he was working at the Arctic Research Laboratory under the sponsorship of the California Institute of Technology and of the Johns Hopkins University through contracts

[1]Received for publication May 16, 1963.

J. Fish. Res. Bd. Canada, **20**(5), 1963.
Printed in Canada.

with the Office of Naval Research (Contract N6onr-243-16). This paper has been prepared in part to provide supplementary information for a study of Antarctic Pycnogonida in progress under Grant 14107 from the National Science Foundation.

I. ZOOGEOGRAPHY

The pycnogonids of the arctic regions fall into three general patterns of distribution. First, there is the boreal-arctic circumpolar type, characterized by the distribution of such species as *Nymphon longitarse*, *Nymphon grossipes* and *Pseudopallene circularis* (Fig. 1). This distribution conforms to Ekman's (1953, p. 176) panarctic type. A second distribution pattern can be recognized for high arctic species in Ekman's sense, with abundant occurrences in deeper water in the boreal zones. Species conforming to this pattern are *Nymphon robustum* and *Colossendeis proboscidea* (Fig. 2), *Nymphon hirtipes* (Fig. 3), and *Nymphon sluiteri*. All of these species are abundant and occur in the high arctic area around the basins between about 120° and 115° E and south as far as Iceland and the Wyville Thomson Ridge. The third type of distribution is the north Pacific boreal pattern, still incompletely known, but characterized by such species as *Achelia borealis* and *Tanystylum anthomasti*. Neither the high arctic nor the boreal north Pacific forms are circumpolar in distribution.

The distribution of pycnogonids therefore, corresponds only approximately to Dunbar's (1953) divisions of the Arctic. His subarctic region (Fig. 4) does

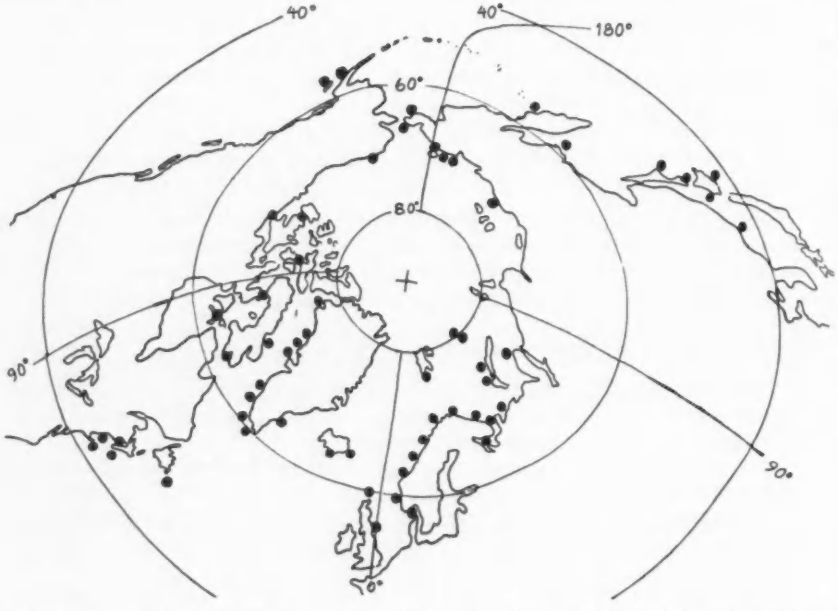


FIG. 1. Distribution of *Nymphon longitarse*. (Principally after Stephensen, 1933, with additions.)

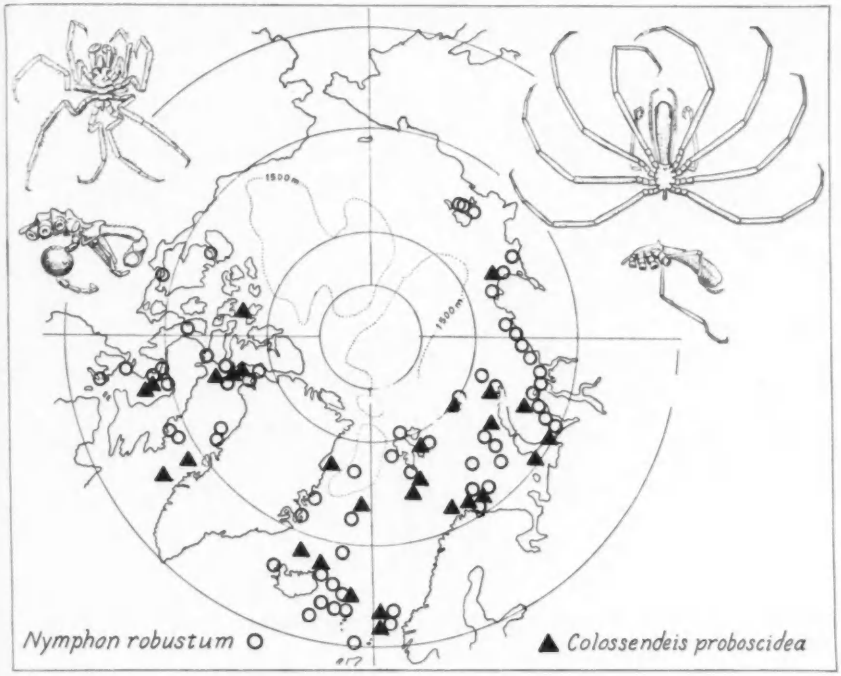


FIG. 2. Distribution of *Colossendeis proboscidea* and *Nymphon robustum*. (From various sources: dorsal views of species slightly less than ½ actual size.)

not include the waters east of Greenland and Baffin Land and the Canadian Archipelago, which are frequented by the high arctic-boreal species. Hudson Bay would also appear to be arctic if we are to judge from the few records of pycnogonids from its waters. His subarctic region for the Atlantic region is more extensive than the distribution of several common species of pycnogonids we might consider boreal non-arctic, such as *Nymphon spinosissimum* and *Pycnogonum littorale* (see Stephensen, 1933, for distribution). There appears to be a similar non-arctic boreal pattern in Pacific waters, but much more collecting is needed in the Bering Sea, Aleutians and southern Alaskan waters to elucidate the significance of the rich pycnogonid fauna of the far eastern seas.

Nesis (1962b) has called attention to a number of species of benthic invertebrates which occur on both coasts of the north Pacific and in the northwestern Atlantic (but not the European shores). These are common species and he finds 13 of them, including mollusks, crustaceans, echinoderms and one ascidian. These amphiboreal species are considered of Pacific origin by Nesis, who suggests that they crossed the Arctic in upper Pliocene times, and are thus to be considered relicts (Fig. 5). I can find no pycnogonid whose distribution conforms to this pattern except possibly *Achelia spinosa*, if this species can be

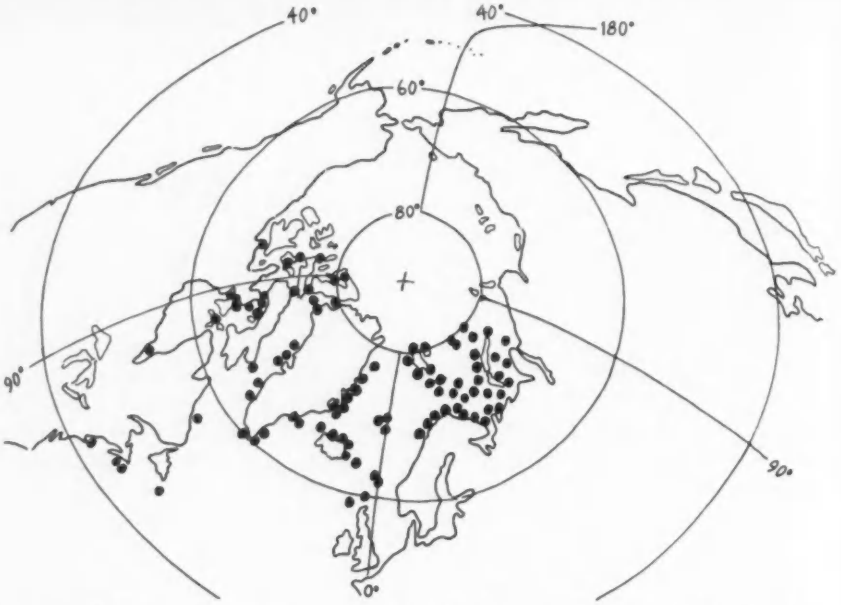


FIG. 3. Distribution of *Nymphon hirtipes* (After Stephensen, 1933, 1934, with additions.)

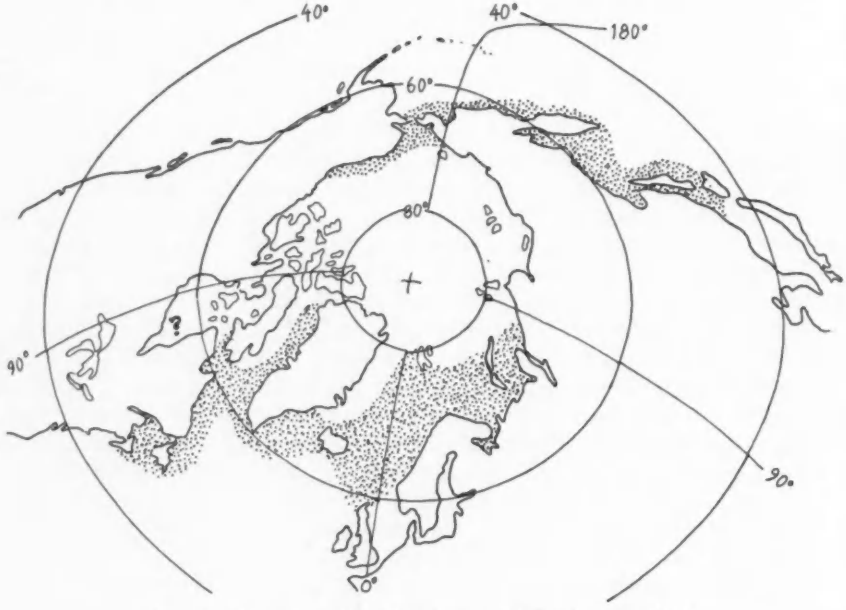


FIG. 4. Subarctic region (dotted), according to Dunbar, 1953.

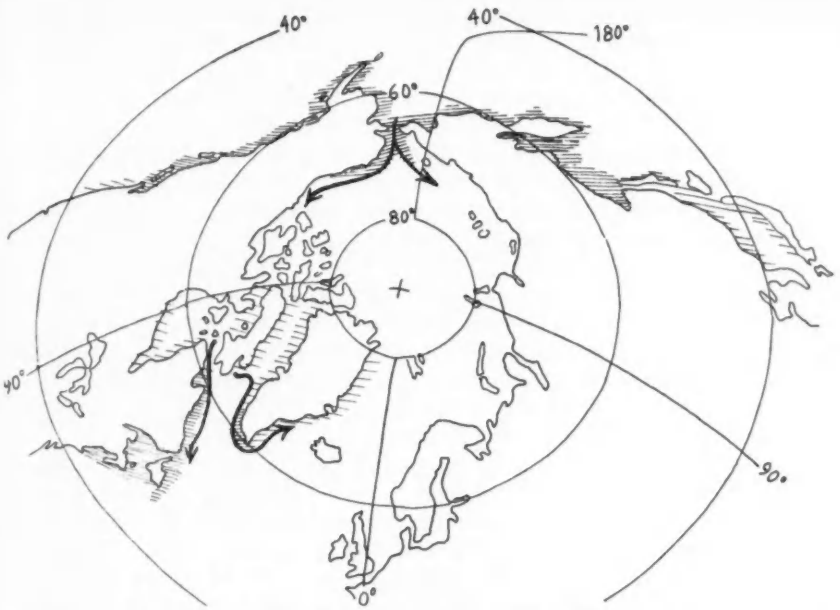


FIG. 5. Mode of migration and distribution of certain amphiboreal species considered to be Pliocene relicts in the western Atlantic (from Nesis, 1962b).

defined as separable from *Achelia echinata*. With the exception of the widely distributed species which are of little use for zoogeographical purposes except to indicate either a rapidly dispersing species or one that resists change, the pycnogonid faunas of the two great boreal to arctic regions of the Atlantic and Pacific are separate and have undergone independent evolution.

The fauna of the Sea of Okhotsk is peculiar, and seems to indicate a separate province of development. Ushakov (1953) listed 29 species and varieties of pycnogonids (25 full species) of which 10, or 35%, were endemic to the Sea of Okhotsk. Losina-Losinsky (1961) has raised the total to 38 species, with 13 endemics, or 40%. From the Soviet far eastern seas altogether (exclusive of the Bering and Chukchi seas) Losina-Losinsky listed 63 species. Several of these, however, will probably turn out to be synonyms. While there may be more species of *Achelia* than will withstand the test of time, it is obvious that the northern Pacific boreal region has many more species in this genus than can be found in the entire north Atlantic. There also appear to be more species of *Pycnogonum*.[2]

The pycnogonid fauna of Greenland, especially of the western coastal regions, appears to be fairly well established (Stephensen, 1933, 1943). Most of the species are the same as found westward into the Arctic Archipelago, and

[2]Losina-Losinsky considers *Pycnogonum tenue* a variety of *P. littorale*; I have considered it (Hedgpeth, 1949) a distinct species.

probably some of the rare species are to be expected farther west. Those species known from west Greenland but not in the arctic waters of Canada are: *Nymphon spinosissimum* (more of a boreal than arctic species), *Nymphon macronyx* (has been recorded off Baffin Land at about 300 m), *Nymphon leptocheles* (incl. possibly *N. groenlandicum*, apparently a rare species of deeper water), *Nymphon macrum* (a north Atlantic deep-water species rarely north of 60°N), *Pallene acus* (a deep water species recorded from Davis Strait at 2258 m), *Pallenopsis calcanea* (although described from Davis Strait between Greenland and Labrador this is really a world-wide bathypelagic species; Hedgpeth, 1962), *Pseudopallene malleolata* (one record at 600 m, 66°35′N, 56°38′W), *Ps. brevicollis* (sparingly taken at several localities from 75–800 m), *Ps. longicollis* (a rare species of the north Atlantic), *Phoxichilidum femoratum* (from the western Greenland coast between 61° and 70°N; no representative of this genus has been collected between western Greenland and Point Barrow!), *Colossendeis angusta* (represented by a single record from the entrance to Jones Sound), *Pycnogonum littorale* (southern Greenland and Gulf of St. Lawrence seem to be the northernmost records on this side of the ocean although the species is found all around Norway to Murmansk), *Pycnogonum crossirostre* (a sparse species, known from Norway, Iceland, New England and midway between Greenland and Baffin Land at 68°N). Most of those species found along west Greenland or in the Davis Strait–Baffin Bay area and not farther westward are really deeper water Atlantic species that have found their way in this area via Davis Strait. The absence of representatives of *Phoxichilidium* and *Pycnogonum* is noteworthy; indeed, no species of *Pycnogonum* has been collected beyond Murmansk on the east, to west Greenland on the west along the rim of the Arctic Ocean.

At two arctic locations there has been intensive nearshore collecting activity. These are the Soviet Biological Station at Murmansk and the Arctic Research Laboratory at Point Barrow. The pycnogonid fauna of the Murmansk region includes many of the common boreal-arctic species of European shores. Three species, the panarctic *Nymphon grossipes*, *Nymphon longitarse* and *Pseudopallene circularis*, occur at both Murmansk and Barrow. They also occur in the Sea of Okhotsk. The remainder of the pycnogonids from Point Barrow show affinity with the north Pacific boreal regions, and, as other writers have observed (e.g. Johnson, 1956), Barrow cannot be considered a truly arctic locality. The several high arctic pycnogonids, all very common, fairly large species do not occur at Point Barrow nor in the Soviet far eastern seas. This seems to be a standard pattern, controlled perhaps in part on the American side by the reduced salinity of the Beaufort Sea (Tully, 1952), and in eastern Siberia perhaps by a similar relationship of the waters to the great Siberian rivers. These effects are probably combined with the prevailing current regime which indicates a correspondingly similar barrier induced by the Beaufort Sea gyral and the southward flow of water towards Greenland from the general region of Novaya Zemlya (see Dunbar, 1960, 1962.)

In his analysis of the scheme to dam the Bering Strait, Dunbar finds that the budget of the Arctic Ocean is approximately in balance, but most of the input

comes from the Norwegian Sea area; only one sixth of the total budget is contributed from the Bering Sea. A general impression of the bulk of the pycnogonid collections, both in numbers of species and in mass (to judge from the frequency of collection of the larger species) indicates that as far as pycnogonida are concerned, the contribution from the Bering Sea is much lower than this. It also appears that the invasion of the waters of the Canadian Archipelago has not been achieved by species from the Beaufort Sea region. Dunbar (1958) calls attention to the possible effects of the tidal forces in the narrow waters of the Canadian Archipelago, and the need for studying these in relation to biological phenomena in the Canadian sector of the Arctic.

Unfortunately there is no information about the pycnogonids of the two deep arctic basins on either side of the Lomonosov Ridge. This is due in part to the difficulty of dragging trawls in this area, as pycnogonids are seldom taken in bottom grabs and do not come to traps as do isopods and amphipods. Doubtless the classic arctic deep water species *Nymphon robustum* and *Colossendeis*

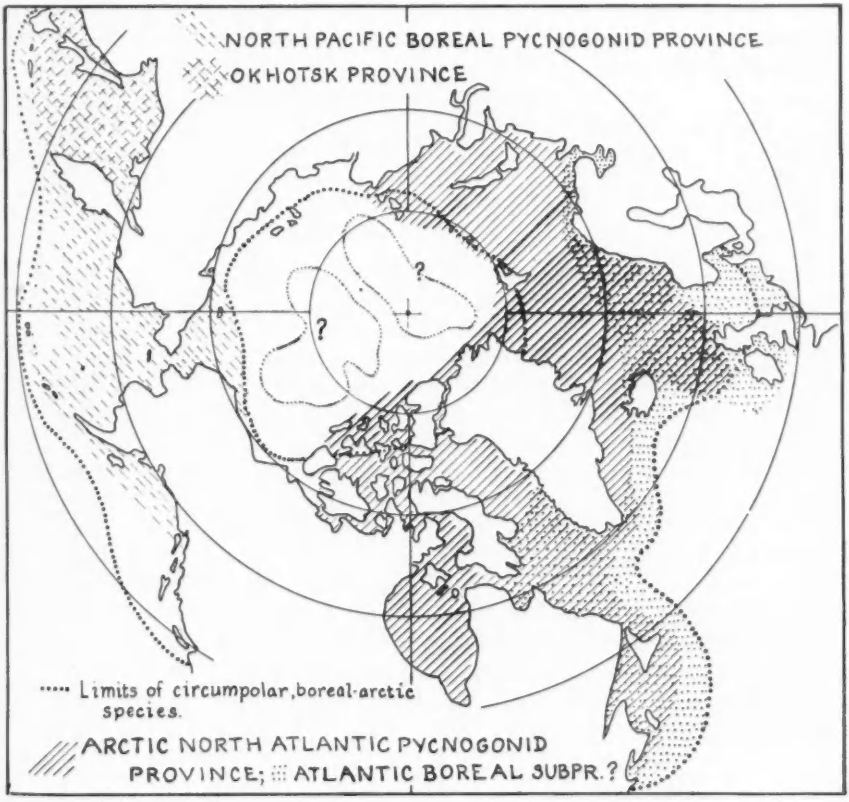


FIG. 6. Pycnogonid provinces of the arctic and boreal regions.

TABLE I. Distribution of Pycnogonida found in arctic waters.

	Canadian Arctic (between Baffin Bay and Beaufort Sea incl. Hudson and Ungava Bays)	W. Greenland (incl. Baffin Bay)	Boreal W. Atlantic, Davis Strait	East Greenland, Iceland	Spitzbergen	N. Norway	Barents Sea, White Sea	Murmansk	Kara Sea	Laptev Sea	East Siberian Sea	Chukchi Sea	Point Barrow	Bering Sea	North Pacific	Sea of Okhotsk
NYMPHONIDAE																
Nymphon robustum Bell	X	X	X	X	X	X	X	X	X	X						
hirtipes Bell	X	X	X	X	X	X	X	X	X	X						
hirtum Krøyer	X			I	X	X	X	X								
macronyx Sars		X	X	X	X	X	X	X	X	X						
spinosissimum (Norman)		X	X	X	X	X										
brevitarse Krøyer	X	X	X		X		X	X					X	X		
rubrum Hodge		X	X		X	X	X	X								
grossipes (Fabr.) Krøyer	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
microrhynchum Sars	X			X			X		X							
longitarse Krøyer	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
sluiteri Hoek	X	X	X	X	X	X	X	X	X							
leptocheles Sars						X	X									
stromi Krøyer	X	X	X	X	X	X	X	X	X	X						
macrum Wilson		X	X	I		X	X	X								
helleri Bohm					X											
elegans Hansen	X	X	X	X	X	X	X		X							
longimanum Sars				X	X		X		X							
micronyx Sars	X	X					X		X							
serratum Sars	X	X	X	X	X	X	X	X	X							
megalops Sars	X	X		I			X									
schimkewitschi Losina-Losinsky					X		X			X						
CALLIPALLENIDAE																
Pseudopallene circularis (Goodsir)	X	X	X	X		X	X	X					X	X	X	X
spinipes (Fabr.)	X	X		I		X	X	X	X	X						
malleolata (Sars)			X	X	X	X	X	X	X							
brevicollis (Sars)		X		I	X	X	X	X	X	X						
longicollis (Sars)			X	X		X										
Pallenopsis arctica Stock					X											
Oropallene polaris n. sp.													X			
PHOXICHILIDIIDAE																
Phoxichilidium femoratum (Rathke)		X	X	X		X	X	X								
quadradentatum Hilton													X	X		
AMMOTHEIDAE																
Achelia spinosa (Stimpson) Wilson			X										X	X	X	X
echinata Hodge							X							X	X	
laevis Hodge				I		X	X	X								X
borealis (Schimkewitsch)									X				X			
Eurycyde hispida (Krøyer)	X	X	X	X		X	X	X	X	X						X
Tanystylum anthomasti Hedgpeth													X		X	
COLOSSENDEIDAE																
Colossendeis proboscidea (Sabine)	X	X	X	X	X	X	X	X	X	X						
angusta Sars	X		X	X			X	X	X	X						
PYCNOGONIDAE																
Pycnogonum littorale (Ström)		X	X	X		X	X	X								
crassirostre Sars		X	X	X		X										

proboscidea occur in these basins, and perhaps also *Colossendeis angusta*. Some surprises from these basins may await us.

It is possible that these larger arctic species may occur in shallower water in areas not adequately sampled: in personal correspondence Losina-Losinsky and Nesis have suggested that these species may be circumpolar at depths below 100 m. These depths have not been investigated adequately in Soviet waters, or in the Beaufort Sea for that matter.

The existence of truly bipolar species of pycnogonids is unlikely, for the whole facies of the pycnogonid fauna of the two polar regions is different. One of the most conspicuous differences is the abundance of large forms in the Antarctic, along with several ten-legged forms, and two twelve-legged forms. No polymerous pycnogonids have been found in the arctic regions, and the only species that might be considered "bi-polar", *Colossendeis angusta*, appears to be fairly widely distributed in deeper waters throughout the world. A whole group of species, the giant Ammotheas, have only one representative in the northern hemisphere, *Ammothea profunda* from the Sea of Okhotsk.

In summary, therefore, we have three well-defined patterns for arctic pycnogonids, with a possible separate pattern for the Sea of Okhotsk (Fig. 6). This provincial scheme cannot be easily applied to other types of distribution patterns. No agreement, for example, appears to exist between this map and that for the provinces of bivalves by Filatova (1957).

II. ECOLOGY

In his study of Greenland Pycnogonida Stephensen (1933) noted the high coincidence of simultaneous occurrences of *Nymphon hirtipes* with the octocoral *Gersemia* (=*Eunephthya*), and found further that at all stations where the octocorals were found, *Nymphon hirtipes* was also found. He also noted that these two organisms had the same general distribution, and concluded that the octocoral was the probable food of the pycnogonid. Although I have no data on the distribution of octocorals between Greenland and the Beaufort Sea, *Gersemia rubiformis* is apparently one of the very common coelenterates in the Point Barrow area (MacGinitie, 1953). *Nymphon hirtipes*, however, does not occur in the Point Barrow region, as we have already seen. In his discussion of the distribution of octocorals in the north Atlantic as related to the hydrographic regime, Nesis (1962a) points out that *Gersemia* is a widely occurring octocoral of Atlantic, Arctic and Pacific waters. Indeed, no species of pycnogonid seems to be as eurytopic as this potential host.

An interesting occurrence of *Gersemia rubiformis* is that in the vicinity of Coos Bay, Oregon (about N lat. 43°21′). At this location the octocoral may be infested with a parasitic or commensal pycnogonid, *Tanystylum anthomasti*. This species was described as infesting an octocoral at Akkeshi Bay, Hokkaido, which was thought to be an *Anthomastus* but is now identified as *Alcyonium pacificum* (see Utinomi, 1954). *Tanystylum anthomasti* occurs at Point Barrow,

but it has not been found on octocorals, although *Gersemia* was taken at the same time on one occasion. It is quite possible that it does infest *Gersemia* at Point Barrow. The known distribution of *Tanystylum anthomasti* is indicated on Fig. 7; this coincides with the occurrence of *Gersemia*.

It is obvious from these examples that we still have some things to learn about the relationships between pycnogonids and coelenterates.

While the implication for the ecology of arctic invertebrates in general is conjectural, it is of considerable interest to note that in three high arctic species of *Nymphon*, *N. robustum*, *N. hirtipes* and *N. sluiteri*, the developing young are carried about by the parent for an apparently long time, until they are quite well developed. In the case of *Nymphon robustum* in particular, young are carried about until they are well over a third the size of the adult. At stations

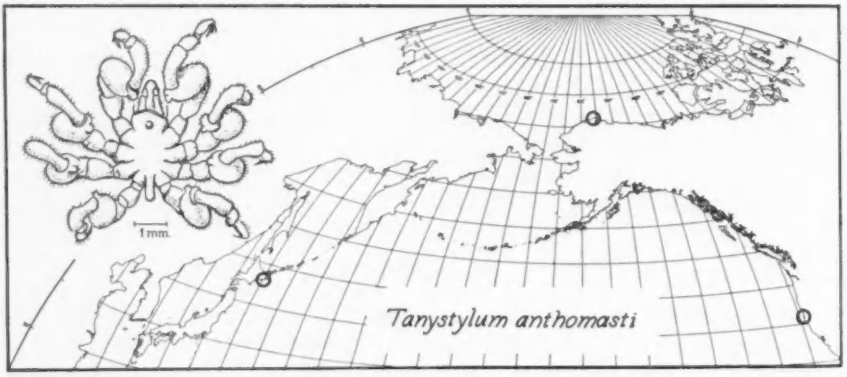


FIG. 7. Distribution of *Tanystylum anthomasti*.

62-2009, 62-2011, 62-2014, 62-2031, and 62-2032 these three species were taken together in the same hauls, and at station 62-3001, these three were the only species taken in seven collections, although all of them were not collected simultaneously. This trait of prolonged carriage of young by the fathers has not been observed for Antarctic pycnogonids.

If these animals breed in summer, as the number of obviously undeveloped egg masses suggests, we would have to assume either that these pycnogonids grow to subadult size in a single season, or that they grow so slowly that the large young specimens being carried about have wintered over with their parents. Possibly hatching occurs in winter, as with the amphipod *Themisto libellula* (Dunbar, 1957). Whatever the reproductive cycle, the matter of nourishment of the young is a most interesting question. Do the fathers carry them about to succulent food, and do the young leave the parents at any time and if so, is it possible that they may return to another father after a feeding foray? How little indeed do we know about these animals!

III. SYSTEMATIC SECTION

Family NYMPHONIDAE Wilson 1878

Genus **Nymphon** J. C. Fabricius 1794

(Including *Boreonymphon* G. O. Sars 1891, and *Chaetonymphon* G. O. Sars 1891)

Nymphon robustum Bell

Boreonymphon robustum Sars 1891, pp. 115–118, pl. 12, fig. 3.
Boreonymphon robustum Stephensen 1933, pp. 4–5, fig. 1.
Nymphon robustum Losina-Losinsky 1935, pp. 16–17.
Boreonymphon robustum Hedgpeth 1943, p. 83.
Boreonymphon robustum Nesis 1960, pp. 16–17.

CALANUS STATIONS:

549, Coll. B-16, 4 IX 53, Evans Strait, N Hudson Bay, 73–75 m, 1 ♀.
612, Coll. B-7, 11 VIII 54, NE Coats Island, N Hudson Bay, 73–75 m, 1 juv.
613, Coll. B-10, 11 VIII 54, NE Coats Island, 198 m, 3 ♂♂ (one with quarter grown larvae,) 1 ♀.
711, Coll. B-10, 8 IX 55, Repulse Bay, 70–100 m, 2 ♂♂ (1 larvig.), 1 ♀.
811, Coll. B-27, 17 VIII 56, Fury & Hecla Strait, 110 m, 1 larvig. ♂.
816, Coll. B-29, 18 VIII 56, Fury & Hecla Strait, 55–80 m, 1 ♀.
818, Coll. B-32, 26 VIII 56, S Tern Island, 95 m, 2 ♂♂, 1 ♀, 4 juv.
820, Coll. B-34, 28 VIII 56, Murray Maxwell Bay, 73 m, 1 ♀.
62-1103, #4, 24 VII 62, Prince of Wales Strait, 26 m, 1 ♀.
62-2008, Coll. B-14, 3 VII 62, Cresswell Bay, 30–45 m, 1 ♂.
Coll. B-15, 5 VII 62, Cresswell Bay, 30–45 m, 8 ♂♂, 1 ♀.
62-2009, Coll. B-26, 25 VII 62, Cresswell Bay, 35 m, 2 ♂♂, 2 ♀♀.
62-2011, Coll. B-25, 24 VII 62, Cresswell Bay, 40 m, 1 ov. ♂, 1 ♀.
62-2012, Coll. B-27, 25 VII 62, Cresswell Bay, 36 m, 1 ♂.
62-2014, Coll. B-30, 25 VII 62, Cresswell Bay, 35 m, 2 ♂♂, 2 imm.
62-2031, Coll. B-44, 11 VIII 62, Cresswell Bay, 40 m, 1 ov. ♂.
62-2032, Coll. B-45, 11 VIII 62, Cresswell Bay, 59–62 m, 1 ♀.
Coll. B-46, 11 VIII 62, Cresswell Bay, 59–62 m, 1 ♀.
62-3001, Coll. B-24, 22 VII 62, Eureka, 12–20 m, 3 juv.
Coll. B-27, 22 VII 62, Eureka, 40–55 m, 1 larvig. ♂.
Coll. B-35, 27 VII 62, Eureka, 30–45-m, 1 ♂.
Coll. B-38, 27 VII 62, Eureka, 2–20 m, 1 ♀.
62-7300, Coll. B-1, 23 VIII 62, S Victoria Island, 30 m, 1 ♂, 1 juv.
62-7302, Coll. B-4, 23 VIII 62, S Victoria Island, 50–60-m, 1 ♂.

This is one of the character species of the high, non-circumpolar arctic distribution pattern, and of the Norwegian Sea north of the Wyville Thomson ridge. One of the best known arctic species, *Nymphon robustum*, was described, in 1855 from collections made during the winter quarters of Belcher's expedition. Since that time, however, very little collecting has been made and these records add many new localities to the known distribution of the species. The record from Station 62-1103 at 118°01′W is the westernmost locality for the Canadian arctic. The bathymetric range of the species is from 10 m in the arctic to depths of over 2000 m in the Norwegian Sea where it may sometimes occur in great abundance (Appelöf, in Murray and Hjort).

The records for ovigerous and larvigerous males are for the summer months July, August and September.

Stephensen suggested this pycnogonid may live on various octocorals, especially *Umbellula*, and also considered the possibility that the smaller in-

dividuals might live on smaller hosts "better fitting the size of the chelae". However, since the young in this species are carried about by the father until they are one fourth to a third as large as the adult, it would not seem that they would have much chance to sample food other than what their fathers carried them to.

There seems little reason to maintain *Boreonymphon* as a separate genus although the species differs from all other Nymphons in the arcuate shape of the dactyls of the chelae, which are smooth and resemble miniature ice tongs.

Nymphon hirtipes Bell

Nymphon hirtipes Bell 1853, p. 403, pl. 35, fig. 3.
Chaetonymphon hirtipes Sars 1891, pp. 103–107, pl. 11, fig. 2a–k.
Chaetonymphon spinosum (partim) Schimkewitsch 1930, pp. 335–365, fig. 81–87.
Chaetonymphon hirtipes Stephensen 1933, pp. 8–9, fig. 2–10.
Nymphon sipinosum var. *hirtipes* Losina-Losinsky 1935, pp. 17–19.
Nymphon hirtipes Hedgpeth 1943, pp. 83, 85.
Nymphon hirtipes Hedgpeth 1948, pp. 183–185, fig. 10b, 11b.
Nymphon spinosum var. *hirtipes* Nesis 1960, pp. 139–140.

CALANUS STATIONS:

613, Coll. B-11, 11 VIII 54, NE Coats Island, N Hudson Bay, 198 m, 2♂♂, 1♀.
711, Coll. B-10, 8 IX 55, Repulse Bay, 70–110 m, 17♂♂ (7 ov.), 23♀♀, 2 juv.
713, Coll. B-13, 12 IX 55, 5 miles S Cape Wilson, 25–49 m, 1♀.
716, Coll. B-15, 19 IX 55, S Tern Island, 92–110 m, 8♂♂, 14♀♀, 10 juv.
722, Coll. B-19, 29 IX 55, Hooper Inlet, 36–45 m, 5♂♂ (2 ov.), 3♀♀, 1 imm.
Spring, 1956. Igloolik Island, from pool in surface ice, 1 ov. ♂.
723, Coll. B-41, 4 IX 56, Turton Bay, 22–24 m, 3♂♂, 2 juv.
811, Coll. B-28, 17 VIII 56, Fury and Hecla Strait, 106 m, 4♂♂ (1 ov.), 12 ♀♀.
815, Coll. , 18 VIII 56, Fury and Hecla Strait, 55 m, 7♂♂ (3 ov.), 3♀♀.
818, Coll. B-32, 26 VII 56, S Tern Island, 95 m, 12♂♂ (3 ov.), 6♀♀, 9 juv.
820, Coll. B-34, 28 VIII 56, Murray Maxwell Bay, 73 m, 2 ov. ♂♂, 3♀♀, 2 juv.
832, Coll. B-44, 8 IX 56, Koh Island to Cape Jensen, 79–90 m, 2♂♂ (1 ov.), 1♀.
837, Coll. B-45, 8 IX 56, Bray Island to Rowey Island, 45–55 m, 1♀.
59-15, Coll. B-13, 10 VII 59, James Bay, 55–60 m, 1 ov. ♂.
61-32, Coll. B-24, 14 VIII 61, SW Foxe Basin, 145 m, 3♀♀.
61-34, Coll. B-25, 23 VIII 61, Repulse Bay, 125 m, 7♂♂ (1 ov.), 8♀♀, 19 imm.
61-36, Coll. B-26, 24 VIII 61, Frozen Strait, 285 m, 3♂♂, 8♀♀, 3 imm.
61-39, Coll. B-27, 25 VIII 61, Duke of York Bay, 42 m, 3♂♂ (1 ov.), 8♀♀.
62-2002, Coll. B-34, 4 VIII 62, Cresswell Bay, 40 m, 3♀♀.
62-2008, Coll. B-14, 3 VII 62, Cresswell Bay, 30–45 m, 1♂, encrusted with sponges and Bryozoa.
62-2009, Coll. B-26, 25 VII 62, Cresswell Bay, 35 m, 1 ov. ♂.
62-2011, Coll. B-24, 23 VII 62, Cresswell Bay, 40 m, 1♂, 1♀.
Coll. B-25, 24 VII 62, Cresswell Bay, 40 m, 1♂, 2♀♀, 3 imm.
62-2012, Coll. B-27, 25 VII 62, Cresswell Bay, 36 m, frags.
62-2014, Coll. B-30, 25 VII 62, Cresswell Bay, 35 m, 6♂♂, 2♀♀, 1 imm.
62-2031, Coll. B-44, 11 VIII 62, Cresswell Bay, 40 m, 2♂♂, 1♀.
62-2032, Coll. B-45, 11 VIII 62, Cresswell Bay, 50–62 m, 2 ov. ♂♂, 2♀♀.
Coll. B-46, 11 VIII 62, Cresswell Bay, 59–62 m, 1 imm.
62-2081, Coll. B-3, 10 IX 62, S Victoria Island, 1 imm.
62-3001, Coll. B-30, 25 VII 62, Eureka, 20 m, 6♂♂, 3♀♀.
Coll. B-36, 27 VII 62, Eureka, 2–30 m, 1 imm.
Coll. B-58, 12 VIII 62, Eureka, 5–30 m, 1♀.

62-3002, Coll. B-12, 11 VII-62, Nansen Sound, 3–5 m, 4♂♂, 5♀♀.
Coll. B-13, 11 VII-62, Nansen Sound, 15–20 m, 2♂♂, 1 imm.
62-4001, Coll. B-46, 6 VIII 62, S Cornwallis Island, 50-m, 2♂♂, 2♀♀.
62-7300, Coll. B-1, 23 VIII 62, S Victoria Island, 30 m, 3♂♂, 1♀, 2 imm.
Coll. B-2, 23 VIII 62, S Victoria Island, 30 m, 1♂.
62-7301, Coll. B-3, 23 VIII 62, S Victoria Island, greater than 30 m, 3♂♂ (1 ov.), 1♀, 1 imm.
62-7302, Coll. B-4, 23 VIII 62, S Victoria Island, 50–60 m, 4♂♂.
62-7305, Coll. B-5, 24 VIII 62, S Victoria Island, 20–30 m, 2♂♂ (1 ov.), 6♀♀, 4 imm.

The arctic distribution of this species is similar to that of *Nymphon robustum*, with the same gap in the far eastern Soviet Arctic and the American Arctic west of about 120°W. The species is found somewhat farther south along the eastern part of America, as far south as Massachusetts Bay. It is a shallow water species in the Arctic and obviously the most abundant and possibly dominant pycnogonid of the Canadian Arctic. The southern records are mostly from fairly deep water but it does not occur as deeply as does *Nymphon robustum*.

For some reason Soviet workers have adopted the usage which reduces the prior name *hirtipes* to varietal status under the partial junior homonym *spinosum*. This may reflect a laudable impulse to make nomenclature conform to their biological concept of the species, but nomenclature has nothing to do with biology, and the situation is further confused by the inclusion of *N. spinosissimum* Norman under this name.

Nymphon hirtum Krøyer

Chaetonymphon hirtum Sars 1891, pp. 101–103, pl. 11, fig. 1.
Chaetonymphon hirtum Schimkewitsch 1930, pp. 327–335, fig. 77–80.
Nymphon hirtum Losina-Losinsky 1935, pp. 19–20.
Chaetonymphon hirtum Stephensen 1943, p. 16.

Calanus St. 832. Coll. B-44, 8 IX 1956, Koh Island to Cape Jensen, 79–90 m, 1♀.

This seems to be the first record of this species west of Iceland. It occurs from Iceland to the Murmansk Sea, along the coast of Norway (but not between 67° and 58°N, according to Stephensen), and as far south as Belgium. Stephensen characterizes it as a "sublittoral, probably boreal species".

Nymphon spinosissimum Norman

Chaetonymphon spinosissimum Stephensen 1933, pp. 6–8, fig. 2.
Chaetonymphon spinosissimum Stephensen 1943, pp. 14–15, fig. 4.
Nymphon spinosissimum Hedgpeth 1948, p. 183, fig. 9, 10a, 11a.

Vema 16-48, 21 VIII 60, 60°10′N, 47°08′W, 300 m, 1♂, 3♀♀.

Stephensen characterized this as a more southerly species than *Nymphon hirtipes*, "with very few occurrences in truly arctic waters". This record from near the southern tip of Greenland is well within the established range of the species, Spitzbergen and Norway, Iceland, and Davis Strait, and south to the Grand Banks.

The synonymy developed by Stephensen (1933) is followed here, as the more spinose aspect and long auxiliary claws make the species easily separable from *N. hirtipes*.

Nymphon brevitarse Krøyer

Nymphon brevitarse Krøyer, 1838.
Nymphon glaciale Lilljeborg, 1851.
Nec *Nymphon brevirostre* Hodge, 1863 (?)
Nymphon gracile Sars 1891, pp. 55–58, pl. 5, fig. 1.
Nymphon brevitarse Sars 1891, pp. 61–65, pl. 5, fig. 3.
Nymphon brevitarse Stephensen 1933, pp. 10–11.
Nymphon brevirostre Losina-Losinsky 1935, pp. 41–57, 102–117.
(*Nymphon brevirostre brevirostre* Losina-Losinsky 1935, p. 47.
Nymphon brevirostre var. *rubrum* Losina-Losinsky 1935, pp. 47–48.
Nymphon brevirostre glaciale f. *typica* Losina-Losinsky 1935, pp. 48–49.
Nymphon brevirostre glaciale f. *caraensis* Losina-Losinsky 1935, pp. 49–50.
Nymphon brevirostre var. *littorale*, Losina-Losinsky 1935, pp. 50–53.
Nymphon brevirostre brevitarse Losina-Losinsky 1935, pp. 53–55.
Nymphon brevirostre var. *spitzbergeniense* Losina-Losinsky 1935, p. 55.
Nymphon brevirostre var. *sibiricum* Losina-Losinsky 1935, pp. 55–57.)
Nymphon brevitarse Hedgpeth 1943, p. 85.
Nymphon brevirostre MacGinitie 1955, p. 170.
Nymphon brevirostre glaciale Nesis 1960, pp. 141–142.
Nymphon brevirostre Losina-Losinsky 1961, pp. 67–69.

CALANUS RECORDS:

44, Coll. P-51, 19 VIII 1947, NE Ungava Bay, 80 m, 1 juv., in plankton tow at 40 m.
129, Coll. P-28, 25 VIII 1949, S Ungava Bay, 15–19 m, 1 ov. ♂.
226, Coll. B-12, 13 VIII 1950, Entr. Hudson Strait, 90–100 m, ov. ♂.
901, Coll. B-31, 26 VII 1957, Frustration Bay, 10 m, 1 ♂.

PT. BARROW RECORDS:

St. 33, 30 VIII 49, 184 ft, 1 ♀, 1 imm.
St. 42, 6 X 49, 216 ft, 1 ♀, 1 imm.
St. 46, 14 X 49, 152 ft, 2 ov. ♂♂, 2 ♀♀, 4 imm.
St. 47, 14 X 49, 175 ft, 8 spec. (♂♂, ♀♀).
9 IX 48, from hydroids on ovigerous ♀ *Hyas*, 1 juv.
9 IX 49, washed ashore, ♀, 2 imm.
22-26 IX 49, washed ashore, 1 ♂.

Also about 30 specimens (none ovigerous) in vials labelled with 3 to 5 separate stations and dates; these usually bear MacGinitie's No. 141.

Most of the specimens here identified as *Nymphon brevitarse* have a cleaner appearance, with the legs more rounded than oval in cross section, with very short terminal segments of the palp and the large spines of the propodus restricted to the proximal half of the sole. The animals are about half to a third the size of *Nymphon grossipes*.

A large part of Losina-Losinsky's 1935 paper is devoted to meristic analysis of abundant material of this variable species from the Soviet arctic regions. Such ratios as proboscis:body length, proboscis:cephalic segment, and the lengths of joints of various appendages were analyzed in painstaking detail. The conclusions of this study are as follows: "*Nymphon glaciale* Lill., *N. rubrum* Hodge, and *N. brevitarse* Krøyer represent forms of the same species, to which we have left the denomination *N. brevirostre*, given it by Hodge for the species inhabiting the districts of Great Britain and the North sea. All specific characters without any exception transgress. . . . *Glaciale* Lilljeborg and *glaciale* Sars, as well as *brevitarse* Krøyer belong to different varieties of *N. brevirostre* (*N.*

brevirostre glaciale f. *typica* (Lill.)., *glaciale* f. *caraensis* (Sars), *brevitarse* f. *minor* and *brevitarse* f. *major*)." While we agree that these various forms and species (except possibly *N. rubrum*) are obviously part of a large, variable species complex of the type common among certain widely distributed pycnogonids, the nomenclature proposed in the above conclusions and followed by later Soviet workers does not agree with the International Rules. Krøyer's name *brevitarse* is the oldest and must be used for the stem species. If the various subspecies, varieties and forms can be clearly separated, some reshuffling of names to be used must be made to agree with the Rules[3].

Nesis (1960) does not agree with this synonymy for *Nymphon rubrum* because of the different pattern of spines on the specimen examined by him. Stock (1955) considers *N. brevirostre* a distinct and well characterized species, as well as *N. rubrum* (see pp. 217–218, under *Nymphon rubrum*), and recognizes *Nymphon gracile* Sars as a synonym of *N. rubrum*.

In view of this tangled synonymy it is not easy to characterize the distribution of this species. However, the pattern of the collections reported here is that of a widespread sublittoral to littoral boreal, low arctic species, including southward ranges to the Sea of Okhotsk and probably the Maritime Provinces of Canada.

Nymphon grossipes (O. Fabr.?) Krøyer

Nymphon grossipes Stephensen 1933, pp. 11–12.
Nymphon grossipes Hedgpeth 1943, pp. 85–86.
Nymphon grossipes Stephensen 1943, pp. 18–20, fig. 6.
Nymphon grossipes Hedgpeth 1943, pp. 85–86.
Nymphon grossipes Hedgpeth 1948, pp. 187–188.
Nymphon grossipes Hedgpeth 1949, p. 247.
Nymphon heterospinum Hedgpeth 1949, pp. 259–260, fig. 27.
Nymphon grossipes Nesis 1960, pp. 142–143.
Nymphon grossipes Losina-Losinsky 1961, pp. 69–70.

CALANUS STATIONS:

203, Coll. B-2, 8 VII 50, SW Ungava Bay, 30 m, 1 ♀.
319, Coll. B-2, 11 VIII 51, Mo. Frobisher Bay, 68–118-m, 1 ov. ♂.
716, Coll. B-15, 19 IX 55, S Tern Island, 92–110, 1 ov. ♂, 1 ♀.
901, Coll. B-50, 24 VIII 57, Frustration Bay, 10 m, 1♂.
60-1035, 25 VIII 60, S Beaufort Sea, 22–44 m, 1♂.
51-1015, 10 VII 61, S Beaufort Sea, 11 m, 1 ♀.

PT. BARROW RECORDS:

St. 20, 5 IX 1948, 1 ov. ♂.
St. 25, 8 VIII 1949, 1 ov. ♂.
St. 27, 9 VIII 1949, 1 ♀.
St. 37, 6 IX 1949, 1 ♀.
St. 42, 6 X 1949, 1♂, 1 ♀.
St. 43, 6 X 1949, 1 spec.
St. 47, 14 X 1949, 1 ♀, 2 juv.
St. 50, 18 II 1950, 1 ov. ♂, 1 juv.

Also numerous specimens "washed ashore"; including ovigerous males on 26 IX 1949 and Oct. 1958, and several vials of specimens bearing multiple station numbers and dates under MacGinitie's field Nos. 230 and 392.

[3]It is interesting to note that Linnaeus is honored on a Soviet postage stamp (1957, 40k. dark brown).

This is the most ubiquitous of all northern hemisphere pycnogonids, as well as the most variable. It is usually found in moderately shallow water throughout the low arctic and boreal regions, southward in the Atlantic to Long Island Sound, and to Puget Sound on the Pacific side. However, it has also been taken from considerable depths (as great as 677 fathoms; Hedgpeth, 1948). Losina-Losinsky is probably correct in reducing *Nymphon heterospinum* Hedgpeth to synonymy under *N. grossipes*· a number of the specimens examined in this study have the spination on the propodus described for *heterospinum*. The record for the Gulf of California (as *Nymphon oculopsinum* Hilton) is still puzzling as no material south of Puget Sound has come to notice; there may have been some label mistake.

The large (about twice the size of the other material) specimens of somewhat heavier build from stations 319, 716 and 61-1015 are recognized here as *Nymphon grossipes mixtum*. Nesis (1960) considers *Nymphon mixtum* a distinct species.

Nymphon microrhynchum Sars

Nymphon microrhynchum Sars 1891, pp. 71–73, pl. 7, fig. 1.
Nymphon microrhynchum Schimkewitsch 1930, pp. 443–445.
Nymphon microrhynchum Stephensen 1933, p. 13.

St. 62-4003, Coll. B-26, 17 VII 62, S Cornwallis Island, 25 mm, 2 ♂♂ (1 ov.), 2 ♀ ♀, 3 imm.

According to Schimkewitsch (who had no material), this species is known only from the White and Kara Seas, and Stephensen questioned earlier records off Baffin Land.

I am not too happy with this determination, but the specimens are definitely not *N. longitarse*, the species with which *N. microrhynchum* could be most easily confused.

Nymphon longitarse Krøyer

Nymphon longitarse Cole 1921, p. 4.
Nymphon longitarse Schimkewitsch 1930, pp. 434–441, fig. 118–120.
Nymphon longitarse Stephensen 1933, pp. 13–14, fig. 3.
Nymphon longitarse Losina-Losinsky 1935, pp. 30–31, fig. 4.
Nymphon longitarse Hedgpeth, 1943, p. 86.
Nymphon longitarse Hedgpeth 1949, pp. 247–248.
Nymphon longitarse Nesis 1960, p. 144.
Nymphon longitarse Losina-Losinsky 1961, p. 65.

CALANUS STATIONS:

520, Coll. P-12, 4 VIII 53, N Mansel Island, 137 m, 1 ov. ♂ (plankton tow at 90 m).
722, Coll. B-19, 29 IX 55, Hooper Inlet, 36–45 m, 1 ov. ♂.
62-1103, #4, 24 VII 62, Prince of Wales Strait, 26 m, 1 ♀.
62-1107, #9, 26 VII 62, Prince of Wales Strait, 16–20 m, 2 ♂♂ (1 ov.).
62-1108, #11, 26 VII 62, Prince of Wales Strait, 50 m, 2 ♀ ♀.
62-4003, Coll. B-26, 17 VII 62, S Cornwallis Island, 25 m, 1 ov. ♂.

PT. BARROW RECORDS (ALL "WASHED ASHORE"):

23 VII 49, 2 spec.; 9–12 IX 49, 1 ♂, 3 ♀ ♀; 12 IX 49, 1 ov. ♂.
26 IX 49, 4 ♂♂ (1 ov.); 2 X 49, 2 ♀ ♀.

This is a comparatively stable species (the principal variation noted is that of somewhat shorter neck and closer lateral processes, Losina-Losinsky's variety

brevicollis) and these records add little to what is at present known of the distribution of the species. It is, as an arctic species, a circumpolar shallow-water form. It also occurs in the Bering Sea, Sea of Okhotsk and Sea of Japan, and near shore along the southwest coast of Hokkaido. In the Atlantic there are a number of records as far south as Cape Cod and the southernmost record is at 39°59′30″ in 425 fathoms south of Cape Cod. It is to be noted that all of MacGinitie's Point Barrow records are from material washed ashore.

Nymphon sluiteri Hoek

Nymphon sluiteri Cole 1921, pp. 3–4.
Nymphon sluiteri Schimkewitsch 1930, pp. 425–434, fig. 113–117.
Nymphon sluiteri Stephensen 1933, p. 14–15, fig. 4.
Nymphon sluiteri Losina-Losinsky 1935, pp. 34.
Nymphon sluiteri Hedgpeth 1943, pp. 86–87.
Nymphon sluiteri Stephensen 1943, pp. 22–24.
Nymphon sluiteri Nesis 1960, p. 144.

CALANUS STATIONS:

62-2003, Coll. B-23, 23 VII 62, Cresswell Bay, 35 m, 2♂♂ (frags.).
62-2009, Coll. B-26, 25 VII 62, Cresswell Bay, 35 m, 1♀.
62-2011, Coll. B-24, 23 VII 62, Cresswell Bay, 40 m, 1♂, 1♀, 2 imm.
62-2011, Coll. B-25, 24 VII 62, Cresswell Bay, 40 m, 2♂♂, 1♀.
62-2014, Coll. B-30, 25 VII 62, Cresswell Bay, 35 m, 1 ov. ♂, 1♀.
62-2031, Coll. B-44, 11 VIII 62, Cresswell Bay, 40 m, 1♂.
62-2032, Coll. B-45, 11 VIII 62, Cresswell Bay, 59–62 m, 1 ov. ♂.
62-3001, Coll. B-24, 22 VII 62, Eureka, 12–20 m, 1 ov. ♂, 2♀♀.
62-3001, Coll. B-27, 22 VII 62, Eureka, 40–55 m, 1♂.
62-3001, Coll. B-30, 25 VII 62, Eureka, 20 m, 1♂ (with late larvae), 1♀.
62-3001, Coll. B-35, 27 VII 62, Eureka, 35–40 m, 1♂, 1♀.
62-3001, Coll. B-36, 27 VII 62, Eureka, 2–30 m, 1♂ (larvig.).
62-3001, Coll. B-58, 12 VIII 62, Eureka, 5–30 m, 1♀.

Although Stephensen (1933) did not think there was much doubt about the circumpolar distribution of this species, it appears to have the same pattern as *Nymphon robustum*, *Nymphon hirtipes* and *Colossendeis proboscidea*. That is, it is a high arctic, non-circumpolar species absent from the Soviet far eastern arctic and from the western American Arctic. It occurs to depths of 1000 m. While not a very common species, it is one of the most easily identified arctic nymphons because of its extremely long, curved terminal claws. It also appears to share the trait of several other arctic species of carrying the young around until they are of fairly large size.

The southernmost record for this species is the Gulf of St. Lawrence (Hedgpeth, 1943).

Nymphon stromi Krøyer

Nymphon stromi Stephensen 1933, pp. 16–17.
Nymphon stromi Hedgpeth 1948, pp. 190–191, fig. 13c.
Nymphon stromi stromi Nesis
Nymphon stromi gracilipes Nesis } 1960, pp. 144–145.

St. 613, Coll. B-11, 11 VIII 54, NE Coats Island, 198 m, 1 ov. ♂ (forma *gracilipes*)
St. 815, Coll. B-29, 18 VIII 56, Fury and Hecla Strait, 55 m, 1♂.

Stephensen characterized this as a widely distributed boreal arctic species "not found along the Arctic America between Baffin Bay and Point Barrow". However, these records extend the range to about 82° W, to the west of Baffin Land. The species is often collected in New England waters and there are two records from deeper water at lat. 30°53′N, well south of Cape Hatteras (Hedgpeth, 1948). Except for these more southerly records, this species has a distribution similar to the classic high arctic species like *Nymphon hirtipes*, but does not appear to be abundant.

Nymphon macrum Wilson

Nymphon macrum Stephensen 1933, pp. 17–18.
Nymphon macrum Hedgpeth 1948, pp. 193–195, fig. 13d, 15.
Nymphon macrum Nesis 1960, pp. 145–146.

Vema St. 16-48, 21 VIII 60, 60°10′N, 47°08′W, 300 m, 3 ♀ ♀, 1 juv.

A species of colder North Atlantic waters, extending as far south as the latitude of Hatteras in deeper water. Stephensen has noted its occurrence off the west coast of Greenland as far north as 67°57′N. This record is from off the southern tip of Greenland.

Nymphon elegans Hansen

Nymphon elegans Stephensen 1933, p. 17.
Nymphon elegans Losina-Losinsky 1935, pp. 22–24, fig. 1.
Nymphon elegans Hedgpeth 1943, p. 86.
Nymphon elegans Stephensen 1943, pp. 24–25.

St. 711, Coll. B-10, 8 IX 55, Repulse Bay, 70–110 m, 1 ♀.

While apparently not too common, this species has a wide distribution in the European Arctic across Russia to about 80° E. There are a number of records around Greenland, and a few records from Foxe Basin were previously published (Hedgpeth, 1943). It is another high arctic, eurybathic species. It was not noted by Nesis (1960) in his study of the pycnogonids from the eastern Murmansk coast.

Nymphon micronyx Sars

Nymphon micronyx Sars 1891, pp. 91–93, pl. 9, fig. 3.
Nymphon micronyx Stephensen 1933, p. 18.
Nymphon micronyx Losina-Losinsky 1935, pp. 29–30.

St. 62-4001, Coll. B-45, 4 VIII 62, S Cornwallis Island, 35 m, 1 ♂, 1 ♀.

Evidently a rare species, not often found. Losina-Losinsky considers Schimkewitsch's determinations under this name for Kamchatka to apply to his concept of *N. brevirostre*. This is the first record for the American Arctic. Stephensen calls it an "apparently very rare species", which "seems to be an arctic littoral species".

While the species may be closely related to the *brevitarse* complex, it does differ in having uniformly finer spines on the appendages and in the longer terminal segment of the palp.

Nymphon serratum Sars

Nymphon serratum Sars 1891, pp. 95–97, pl. 10, fig. 2.
Nymphon serratum Stephensen 1933, pp. 18–19.
Nymphon serratum Losina-Losinsky 1935, p. 25.
Nymphon serratum Hedgpeth 1943, p. 87.
Nymphon serratum Nesis 1960, p. 146.

CALANUS STATIONS:

613, Coll. B-9, 11 VIII 54, NE Coats Island, 144–162 m, 1 ♀.
711, Coll. B-10, 8 IX 55, Repulse Bay, 70–110 m, 1 ♂.
811, Coll. B-27, 17 VIII 56, Fury & Hecla Strait, 110 m, 2 ♂♂, 2 ♀♀, 1 juv.
837, Coll. B-45, 8 IX 56, Bray Island, to Rowey Island, 45–55 m, 1 ♀.
59-15, Coll. B-13, 10 VII 59, James Bay, 55–60 m, 1 ♀.

Stephensen characterized this as "a mainly arctic, sublittoral species". These records extend its known range somewhat to the west of Foxe Basin. It is interesting to note that the record for James Bay is the second collection of this species in the southern part of Hudson Bay, the earlier one being that for Station 31 of the Hudson Bay Fisheries Expedition in 1930.

Nymphon megalops Sars

Nymphon megalops Sars 1891, pp. 98–100, pl. 10, fig. 3.
Nymphon megalops Stephensen 1933, p. 19.
Nymphon megalops Hedgpeth 1943, pp. 87–88, fig. 2.

719, Coll. B-18, 29 IX 55, Hooper Inlet, 51 m, 1 ov. ♂.
815, Coll. B-29, 18 VIII 56, Fury & Hecla Strait, 55 m, 1 ov. ♂.
818, Coll. B-32, 26 VIII 56, S Tern Island, 95 m, 1 ♂.

Characterized by Stephensen as "an arctic deep sea species". These records are from depths of 51–106 m, which would suggest that in the American Arctic this is a sublittoral species.

Family CALLIPALLENIDAE Hilton 1942

Genus **Pseudopallene** Wilson, 1878

Pseudopallene circularis (Goodsir)

Pseudopallene circularis Sars 1891, pp. 38–42, pl. 3, fig. 3.
Pseudopallene circularis Schimkewich 1930, pp. 260–270, fig. 62–66.
Pseudopallene circularis Stephensen 1933, pp. 20–21.
Pseudopallene circularis Losina-Losinsky 1935, p. 12.
Pseudopallene setosa Hilton 1942, p. 39.
Pseudopallene spinosa Hilton 1942, p. 39.
Cordylochele setospines Hilton 1942, p. 39.
Cordylochele microspines Hilton 1942, p. 39.
Pseudopallene circularis Hedgpeth 1943, p. 88.
Pseudopallene circularis Stephensen 1943, p. 26.
Pseudopallene circularis Hedgpeth 1948, p. 206, fig. 19.
Pseudopallene circularis Nesis 1960, p. 146.

CALANUS STATIONS:

3, Coll. P-8, 29 VI 47, S Ungava Bay, 28 m, 1 ♀.
723, Coll. B-41, 4 IX 56, Turton Bay, 22–24 m, 1 juv.
61-10, 30 VII 61, Chesterfield Inlet, 75–90 m, 1 ov. ♂.

PT. BARROW RECORDS:

Sts. 17-21, 9-15 IX 48, No. 390, 1♂, 2♀♀, 2 juv.
St. 24, 16 IX 48, 1 juv.; St. 27, 9 VIII 49, 3 juv.; St. 33, 30 VIII 49, 1 juv.; St. 37, 6 IX 49, 2 juv.; St. 44, 11 X 49, 1♂, 4 juv.; St. 45, 11 X 49, 1♂, 1 juv.; St. 47, 14 X 49, 1 juv.
Burton Island, St. 16, 21 II 51, Bering Sea, 30 m, 1 juv.

This is a widely distributed boreal arctic littoral species.

Examination of the specimens upon which Hilton proposed several species of *Pseudopallene* and *Cordylochele* indicates that all this material is *Pseudopallene circularis* in various growth stages. The records are from the Bering Sea and the Aleutians. (Albatross Station 4791 is correctly given as 166°50′15″E instead of 166°58′15″E.)

Pseudopallene spinipes (Fabr.)

Pseudopallene spinipes Stephensen 1933, p. 21.
Pseudopallene spinipes Losina-Losinsky 1935, pp. 11–12.
Pseudopallene spinipes Hedgpeth 1943, p. 88.
Pseudopallene spinipes Nesis 1960, pp. 146–147.

33, Coll. B-15, 10 VII 47, E Ungava Bay, 18–27 m, 1♂.

This is not a common species, and its distribution appears to be somewhat restricted. This is the westernmost record so far; the species is known from localities eastward to the Kara Sea. It is sublittoral, with records to 380 m, but most of them at lesser depths.

Genus **Oropallene** Schimkewitsch 1930

Oropallene Schimkewitsch 1930, pp. 291–292.
Oropallene Stock 1954, pp. 28–31.

Oropallene polaris n. sp. (Fig. 8).

Pt. Barrow, St. 42, 6 X 1949, 4.3 miles out, 216 ft, rocks, stones. 1♂ (Holotype, U.S.N.M. No. 109528), 1 juv. G. E. MacGinitie, Coll.

DESCRIPTION

A small, clean-limbed species without conspicuous spines except for a tuft at the base of the dactyl of the chela. Trunk with well-separated lateral processes, neck constricted but heavy, broadened anteriorly to support the rather heavy chelifores. Eye tubercle erect, at the middle of the cephalic segment, diameter about $\frac{2}{3}$ the height, rounded. Eyes large, moderately pigmented. Abdomen short, erect but slanting on a steep angle, in this specimen cleft at the end.

Chelifores heavy, scape and chelae subequal. Claws flat, thin-bladed, with teeth at base and serrations toward the crossed tips. Palp small four-jointed, first joint slightly longer than second, fourth shorter than second. A few spines on ventral surface. Oviger ten-jointed, but without the prominent process on the fifth joint, fourth and fifth joints longest, spines present only on terminal joint, leaflike with basal serrations larger. Terminal spine of oviger large, bifid.

Legs moderately stocky, without heavy spines or knobs. The propodus bears three or four large spines on the sole but does not have a well-developed heel. There is a blunt, heavy terminal claw flanked by two large auxiliaries about half the length of the terminal claw.

MEASUREMENTS	*mm*		*mm*
Trunk	1.2	Third leg	4.28
First trunk segment	0.625	First coxa	0.18
Width, second trunk segment	0.7	Second coxa	0.3
		Third coxa	0.25
Abdomen	ca. 0.5		
		Femur	0.85
Chelifore: Scape	0.45		
		First tibia	0.85
Chela	0.45		
		Second tibia	1.15
Palpus	0.55		
		Tarsus	0.2
Oviger	ca. 1.2		
		Propodus	0.5
		Ter. claw	0.23
		Aux. claw	0.13

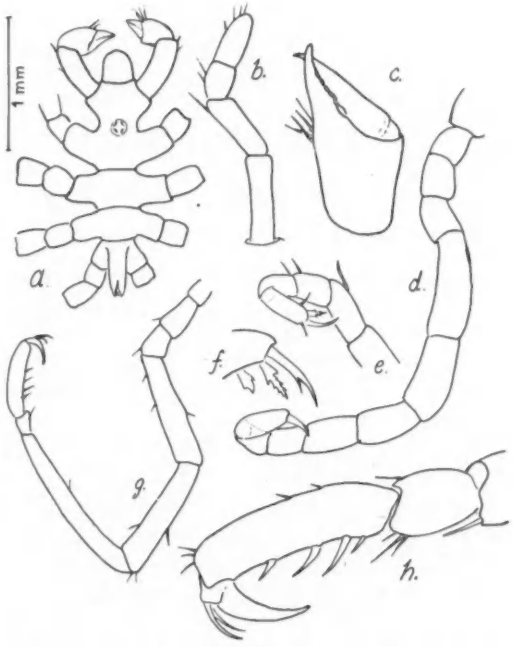


FIG. 8. *Oropallene polaris*, n.sp.; *a*, dorsal view of body; *b*, palpus; *c*, chela; *d*, oviger; *e*, terminal segments of oviger; *f*, spines of oviger; *g*, third leg; *h*, tarsus and propodus (all drawings from holotype).

Discussion

This seems to be the only species in addition to the genotype *Oropallene dimorpha* (Hoek, 1898, from Kerguelen) that agrees with the diagnosis of the genus established by Schimkewitsch (1930), namely in having a terminal claw on the oviger, four-jointed palpi in the male, and auxiliary claws on the tarsus. It lacks a prominent apophysis on the fifth joint of the oviger.

This species differs from *Oropallene dimorpha* in lacking heavy spines on the appendages and also in lacking prominent tubercles on the distal margins of the lateral processes. The sole of the propodus of *O. dimorpha* bears a row of equal spines in contrast to the few large spines in *O. polaris*. The paucity of special spines and lack of apophysis on the fifth joint of the oviger suggests that the type specimen may not be fully adult. The juvenile specimen has only three well-developed pairs of legs and long buds for the fourth pair.

Stock (1954) has commented on the uncertain affinity of several species referred to *Oropallene*; I agree with him that most of the species assigned to this genus destroy the definition as established by Schimkewitsch.

The status of *Oropallene ovigerosetosa* Hilton (1952b) is uncertain since the only specimen is a female. I have not been able to examine the type specimen.

Family PHOXICHILIDIIDAE Sars, 1891

Genus **Phoxichilidium** Milne-Edwards, 1840

Phoxichilidium quadradentatum Hilton (Fig. 9)

Phoxichilidium quadradentatum Hilton 1942b, p. 71.

Eluitkak Pass, Elson Lagoon, 10 VIII 48, stony mud, among hydroids and bryozoans, 1 ov. ♂.

This is a large, robust specimen, about three times the size of the type (from Stewart Island, Alaska). In the structure of the heel spines this species resembles *Ph. tubulariae* Lębour (1945) from Plymouth, but that form is much smaller. The status of these specimens may be resolved by critical examination of a large series; these names may represent variations of *Phoxichilidium femoratum*. A large mass of material assigned to *Ph. quadradentatum* was collected some years ago off the Golden Gate near San Francisco during a fouling survey, but I have been unable to find the time to examine it critically. A sampling of the specimens indicated that the spination of the heel of the propodus agreed with this species.

I am guilty of incorrectly publishing this name as *quadridentatum* in a faunal handbook (Light *et al.*, 1954) from the way it was spelled on the label, although it was published as *quadradentatum*.

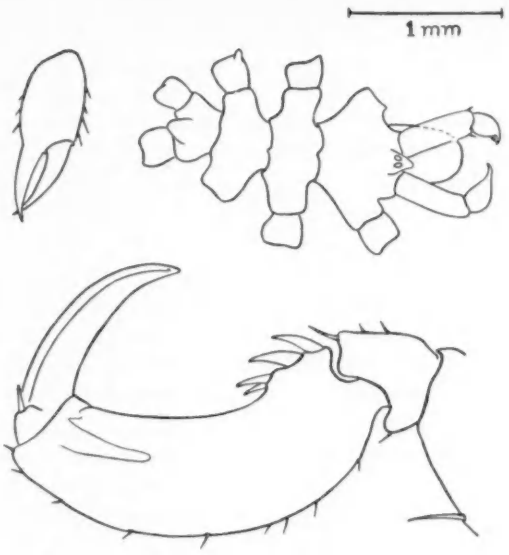


FIG. 9. *Phoxichilidium quadradentatum* Hilton: *a*, trunk; *b*, chela; *c*, tarsus and propodus (drawings from holotype).

Family AMMOTHEIDAE Dohrn 1881

Genus **Achelia** Hodge, 1864

Achelia spinosa (Stimpson) Wilson

Ammothea (*Achelia*) *echinata* var. *spinosa* Schimkewitsch 1929, pp. 133–135.
Ammothea lavrentii Losina-Losinsky 1933, pp. 49–50, fig. 3.
Ammothea uschakovi Losina-Losinsky 1933, pp. 50–52, fig. 4.
Ammothea litke Losina-Losinsky 1933, pp. 52–53, fig. 5.
Achelia spinosa Hedgpeth 1948, pp. 242–245, fig. 38a–b. (Synonymy).
Achelia spinosa Stock 1954, p. 96.

PT. BARROW RECORDS:

St. 20, 9 IX 48, 2 juv.; St. 33, 30 VIII 49, 1 ♀, 1 juv.; St. 35, 1 IX 49, 1 juv.; St. 37, 6 IX 49, 2 juv.; St. 41, 6 X 49; 1 ♂; St. 42, 6 X 49, 1 ♀; St. 44, 11 X 49, 2 ♂♂, 2 ♀♀, 1 juv.; St. 45, 11 X 49, 1 ♂, 1 juv.; St. 47, 3 ♂♂ (1 ov.) 4 ♀♀, 2 juv.; St. 50, 18 II 50, 1 ♀.

This species is characterized by heavy spinose tubercles on the coxae, lack of trunk segmentation and long auxiliary claws. As previously noted (Hedgpeth, 1948) some European workers have considered *spinosa* to be a synonym or variety of *A. echinata*. There are many records for a heavily spinose *Achelia* with two suture lines on the trunk from Japan, Sea of Okhotsk and one record off San Francisco, in addition to the European distribution assigned to *Achelia echinata*. It is possible that *Achelia spinosa* and *echinata* are indeed synonymous since the

only clear distinctions are the segmented trunk and possibly longer genital spurs of the forms assigned to *A. echinata*. (*A. spinosa*, however, is the older name.) If this is the case, we are dealing with a variable species similar to the southern hemisphere *Achelia assimils* Haswell (see Hedgpeth, 1961). The most conspicuous difference between these two complexes is the absence of dorsal trunk tubercles from the northern hemisphere group.

In any event, *Achelia spinosa* as I understand it occurs on the cold Atlantic coast of North America, Sagami Bay (Stock, 1954), the Bering Sea and Point Barrow.

The several species described by Losina-Losinsky are based on the two sexes and juveniles; all the material was collected at the same place on the same date (Lavrenti Bay, Bering Sea, 14 IX 1929). The material from Point Barrow is very similar: the males agree with *A. lavrentii* (described from a male), the females with *A. uschakovi* (described from a female) and the juveniles with *A. litke* and its variety *intermedia* (based on immature material).

It would seem that someone could be persuaded to gather more precise information about the natural history of the various forms assigned to *Achelia echinata* along the coasts of Europe and in Japanese waters. Pending such information, it seems best only to indicate the possibility of this synonymy. Preliminary studies have indicated that the pycnogonids are refractory material for modern statistical treatment, as there are so many possible combinations of characters that selection of any group of them for analysis is bound to be based on our understanding of the limits of the species. This leads us down a circular primrose path.

The north Pacific littoral regions appear to be more richly endowed with species of *Achelia* than other parts of the world, and the numbers of species are a striking contrast to the few found in the north Atlantic.

Achelia borealis (Schimkewitsch)

Ammothea borealis Schimkewitsch 1895 pp. 36–40, pl. 2, fig. 4–6.
Ammothea (*Achelia*) *borealis* Schimkewitsch 1930, pp. 139–144, fig. 34–37.
Achelia borealis Hedgpeth 1949, pp. 286–287, fig. 41 h–m.
Ammothea borealis var. *japonica* Losina-Losinsky 1933, pp. 57–59, fig. 9.
Ammothea borealis Losina-Losinsky 1935, pp. 59–61, fig. 7–8.

Pt. Barrow Records:

St. 17, 9 IX 48, 1 ♀; St. 47, 14 X 49, 1 ♀.
Washed ashore, 12 IX 49, 1 ov. ♂; 2 X 49, 1 ov. ♂ (with almost hatched larvae).

The rather short, bluntly terminated proboscis and long slender propodus are characteristic features of this material, and agree more completely with the original description than the specimen illustrated by me in 1949, which was somewhat abnormal (it had only three legs on one side), and was perhaps from an unusual depth. This species is not reported in more recent Soviet studies.

Genus **Eurycyde** Schiodte, 1857

Eurycyde hispida (Krøyer)

Eurycyde hispida Sars 1891, pp. 128–132, pl. 14, fig. 1.
Eurycyde hispida Stephensen 1933, p. 27.
Eurycyde hispida Losina-Losinsky 1935, pp. 61–62.
Eurycyde hispida Hedgpeth 1943, p. 88.
Eurycyde hispida Stephensen 1943, p. 28.

St. 203, Coll. B-2, 8 VII 50, SW Ungava Bay, 30 m, 1♂.

In 1933 Stephensen characterized this as an "arctic littoral-sublittoral species", but in 1943 he listed it as "a low arctic (?) species". It seems to be widely and sparsely scattered from the eastern fringe of arctic Canada to the Kara Sea.

Genus **Tanystylum** Miers, 1879

Tanystylum anthomasti Hedgpeth (Figure 7, 10)

Tanystylum anthomasthi Hedgpeth 1949, pp. 297–298, fig. 45.
Tanystylum arthomasthi Utinomi 1954, pp. 23–26, fig. 10–11, pl. 1, fig. 2.

Pt. Barrow. G. E. MacGinitie, Coll.:
St. 10, 23 VIII 1948, 150 ft, 1♀.
St. 20, 9 IX 1948, 125 ft, 1♀.
St. 37, 6 IX 1949, 7.5 miles out, 217 ft, stones, large, perf. rocks. 1♂.

Off Coos Bay Entrance, Oregon, 15 VII 1958. Between Baltimore Buoy and Rock, 13 fathoms dredge no. 2. J. A. MacNab, coll. Several immature and female specimens, on *Gersemia rubiformis*.

The name for this species was proposed in manuscript by Professor Ohshima because it occurred on the octocoral *Anthomastus*, but it appears that the host of the original material is actually *Alcyonium pacificum*, according to Utinomi, who has examined more material of this pycnogonid from Akkeshi Bay. The above records are the first outside of Japan, and indicate that the species is not restricted to one species of octocoral. According to MacGinitie's description (1955, p. 74) of his Station 37 *Eunephthya* (= *Gersemia*) *rubiformis* occurred at the same area. The other Pt. Barrow finds came from his stations 10 and 20, for which MacGinitie did not note the octocoral, but did comment on the abundance of bottom life. Perhaps this pycnogonid is not restricted to octocorals, and it may not be rare between Oregon and Alaska. It would appear to be an amphipacific boreal-arctic species (Fig. 7).

Utinomi has completed the description of this species, including that of the male. He comments on the twisted condition of the oviger, and the accompanying illustration (Fig. 10) shows this structure from the Pt. Barrow male from a different angle. Apparently the terminal spines of the oviger lack serrations, although it is difficult to determine this.

Tanystylum anthomasti appears to be a rather uniform and well-characterized species. In the preserved specimen of *Gersemia rubiformis* from Oregon individual pycnogonids were scattered over the surface and deep between the lobes. Solitary individuals could easily be overlooked, and it is possible that there may be more specimens in MacGinitie's octocoral material. Several specimens of

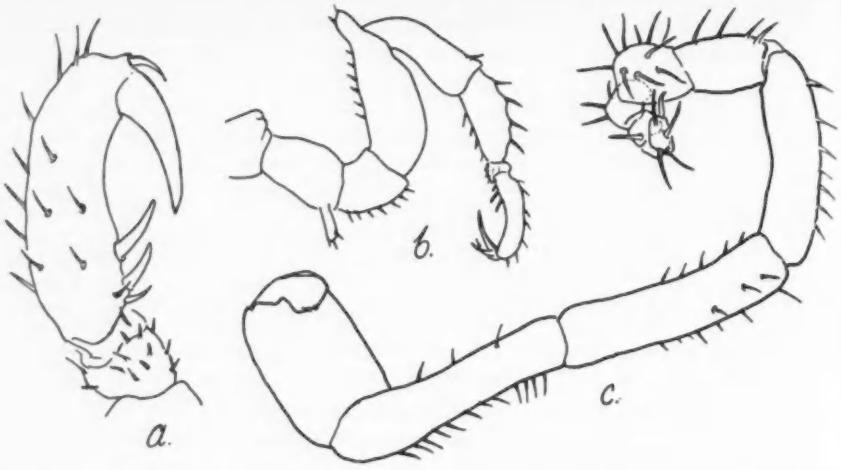


FIG. 10. *Tanystylum anthomasti* Hedgpeth: *a*, tarsus and propodus; *b*, leg of male; *c*, oviger.

Gersemia collected in Oregon were infested, and the species is apparently common there, as it seems to be in Akkeshi Bay.

Family COLOSSENDEIDAE Hoek, 1881

Genus **Colossendeis** Jarzynsky, 1870

Colossendeis proboscidea (Sabine)

Colossendeis proboscidea Sars, 1891, pp. 138–140, pl. 15, fig. 1.
Colossendeis proboscidea Schimkewitsch, 1930, pp. 27–39, fig. 6.
Colossendeis proboscidea Stephensen 1933, p. 28, fig. 6, 9.
Colossendeis proboscidea Hedgpeth 1943, pp. 88–89.
Colossendeis proboscidea Stephensen, 1943, p. 28.
Colossendeis proboscidea Nesis 1960, pp. 137–148, fig. 2.

St. 818, Coll. B-32, 26 VIII 56, South of Tern Island, 95 m, 1 ♀ (with detached proboscis).

This record extends the distribution of this characteristic high Arctic but not circumpolar species somewhat south into the Canadian Archipelago. Its known distribution is charted on Fig. 2. This is the largest species in the Arctic basin, but several antarctic species of this genus are larger, and some of the abyssal species are the largest pycnogonids known. As yet, however, we are in complete ignorance of the reproductive cycle of this entire genus as no ovigerous males or obviously ripe females have been collected.

Colossendeis angusta Sars

Colossendeis angusta Stephensen 1933, pp. 28–29, fig. 6–7.
Colossendeis angusta Hedgpeth, 1948, pp. 269–271.
Colossendeis angusta Hedgpeth 1949, pp. 298–299.
Colossendeis angusta Nesis 1960, p. 148.

(Not represented in the collections.)

This species was collected by the Godthaab expeditions at the entrance of Jones Sound at 75°54′N, 81°01′W, which places it within the American arctic area. While it may occur in one or both deep arctic basins, it evidently is not to be found within the shallow interisland areas of the Canadian Archipelago. It is a world wide deep water (but not abyssal) species of the Atlantic and Pacific oceans and also approaches the antarctic regions. Because of its wide distribution, it cannot be considered a "bipolar" species.

REFERENCES

COLE, LEON J. 1921. Report on Pycnogonida collected by the Canadian Arctic Expedition, 1913–1918. Crustacea, Part F. *Rept. Canadian Arctic Exp.*, **7**.

DUNBAR, M. J. 1953. Arctic and subarctic marine ecology: immediate problems. *Arctic*, **6**(2): 75–90.

1957. The determinants of production in northern seas: A study of the biology of *Themisto libellula* Mandt. Calanus Series No. 14. *Canadian J. Zool.*, **35**: 797–819.

1958. Physical oceanographic results of the "Calanus" Expeditions in Ungava Bay, Frobisher Bay, Cumberland Sound, Hudson Strait and northern Hudson Bay, 1949–1955. *J. Fish. Res. Bd. Canada*, **15**(2): 155–201.

MS, 1960. Preliminary report on the Bering Strait scheme. *Northern Coordination and Research Centre*, 60–1, 14 pp.

MS, 1962. Second report on the Bering Strait dam. *Ibid.*, 62–6, 23 pp.

DUNBAR, M. J., AND E. H. GRAINGER. 1952. Station list of the "Calanus" Expeditions, 1947–1950. *J. Fish. Res. Bd. Canada*, **9**(2): 65–82.

EKMAN, SVEN. 1953. Zoogeography of the sea. Sidgwick and Jackson, London. 417 pp., 121 fig.

FILATOVA, Z. A. 1957. Zoogeograficheskoe raionirovanie severnykh morei po rasprostraneniiu dvustvorchatykh molliuskov. [Zoogeographical regions of the arctic ocean according to distribution of bivalve mollusks.] *Trudy Instituta Okeanologii*, **23**: 195–215.

GRAINGER, E. H. 1954. Station list of the *Calanus* Expeditions, 1951–52, together with Frobisher Bay stations, 1948, 1950 and 1951, and Resolution Island stations, 1950. *J. Fish. Res. Bd. Canada*, **11**(1): 98–105.

GRAINGER, E. H., AND J. G. HUNTER. 1959. Station list of the 1955–58 field investigations of the Arctic Unit of the Fisheries Research Board of Canada. *J. Fish. Res. Bd. Canada*, **16**(4): 403–420.

HEDGPETH, JOEL W. 1943. Pycnogonida of the Bartlett Collections. *J. Washington Acad. Sci.*, **33**(3): 83–90.

1948. The Pycnogonida of the western North Atlantic and the Caribbean. *Proc. U.S. Nat. Mus.*, **97**: 157–342.

1949. Report on the Pycnogonida collected by the Albatross in Japanese waters in 1900 and 1906. *Ibid.*, **98**: 243–321.

1961. Pycnogonida. *Rept. Lund Univ. Chile Exp.*, No. 40, *Lunds Univ. Arssk.* N. F. Avd. 2, **57**(3): 18 pp.

1962. A bathypelagic pycnogonid. *Deep-Sea Research*, **9**: 487–491.

HILTON, W. A. 1942a. Pantopoda (Continued). II — Family Callipallenidae. *Pomona J. Ent. and Zool.*, **34**(2): 38–41.

1942b. Pycnogonids from Hawaii. *Occasional Papers Bishop Mus.*, **17**(3): 43–55.

1942c. Pycnogonids from the Pacific. Family Phoxichilididae Sars 1891. *Pomona J. Ent. and Zool.*, **34**(3): 71–74.

HYDROGRAPHIC OFFICE, U.S. NAVY. 1958. Oceanographic atlas of the polar seas. Part II. Arctic. Washington, H. O. Publ. No. 705, 149 pp.

JOHNSON, MARTIN W. 1956. The plankton of the Beaufort and Chukchi Sea areas of the Arctic and its relation to the hydrography. *Arctic Inst. North Amer., Tech. Paper* 1, 32 pp.

LEBOUR, MARIE V. 1945. Notes on the pycnogonida of Plymouth. *J. Mar. Biol. Assoc. U.K.*, **26**: 139–165.

LIGHT, S. F., *et al.* 1954. Intertidal invertebrates of the Central California Coast. University of California Press, Berkeley. xiv + 446 pp., 138 fig.

LOSINA-LOSINSKY, L. K. 1933. Pantopoda vostochnykh morei SSSR. [Die Pantopoden der östlichen Meere der USSR.] *Issledovanie Morei SSSR*, **17**: 43–80. [German summary, pp. 74–79.]

1935. Pantopoda arkticheskikh morei SSSR. [Pantopoda of the polar seas within USSR.] *Vsesoiuznyi Arkticheskii Inst.*, (*Materialy dlia Izuchenii Arktiki*), No. 4, 140 pp.

1961. Mnogokolenchatye (Pantopoda) dalnevostochnykh morei SSSR. [Pantopoda of the far eastern seas of USSR.] *Issledovanie Dalnevostochnykh Morei SSSR*, **7**: 47–117.

MACGINITIE, G. E. 1955. Distribution and ecology of the marine invertebrates of Point Barrow, Alaska. *Smithsonian Misc. Collections*, **128**(9): 201 pp.

MURRAY, JOHN, AND JOHAN HJORT. 1912. The depths of the ocean. Macmillan, London, 821 pp. (Chap. 8, pp. 457–560, "Invertebrate bottom fauna of the Norwegian Sea and North Atlantic", by A. Appelöf.)

NESIS, K. N. 1960. Pantopoda pribrezh'ya vostochnogo Murmana. [Pantopoda of the coast of eastern Murmansk.] *Trudy Murmanskogo Biologicheskogo Instituta*, **2**(6): 137–161.

1962a. Korally i morskie per'ya — indikatory gidrologicheskogo rezhima. [Corals and sea pens — indicators of the hydrological regime.] *Okeanologiya*, **2**(4): 705–714.

1962b. Tikhookeanskie elementy v bentose severo-zapnoi Atlantiki. [Pacific elements in northwestern Atlantic benthos.] [Soviet Fisheries Investigations in the Northwestern Atlantic], pp. 83–98. VNIRO-PINRO, Moscow.

ROSS, J. C. 1826. *In* Parry's Journal of a third voyage for the discovery of a north-west passage from the Atlantic to the Pacific, performed in the years 1824–25. Appendix: 91–120.

SARS, G. O. 1891. Pycnogonidea. *Norwegian North Atlantic Expedition* **6** (Zoology 20), 163 pp.

SCHMIKEWITSCH, W. M. 1930. Mnogokolenchatye (Pantopoda). [Pantopodes (Pantopoda).] Fauna, SSSR, 544 pp. (No. 1, 1929; No. 2, 1930.)

STEPHENSEN, K. 1933. The Godthaab Expedition 1928. Pycnogonida. *Medd. Grønland*, **79**(6): 46 pp.

1943. The zoology of East Greenland. Pycnogonida. *Ibid.*, **121**(8): 41 pp.

STOCK, J. H. 1954. Pycnogonida from Indo-West Pacific, Australian, and New Zealand waters. *Vidensk. Medd. fra Dansk Naturh. Foren.*, **116**: 1–168.

1955. Pycnogonida from the West Indies, Central America, and the Pacific Coast of North America. *Ibid.*, **117**: 209–266.

1956. Pantopoden aus dem Zoologischen Museum Hamburg. *Mitt. Hamburg. Zool. Mus. Inst.*, **54**: 33–48.

TULLY, JOHN P. 1952. Oceanographic data of the western Canadian arctic region, 1935–37. *J. Fish. Res. Bd. Canada*, **8**(5): 378–382.

USHAKOV, P. V. 1953. Fauna Okhotskogo Morya i usloviya ee sushchestvovaniya. [Fauna of the Sea of Okhotsk and its conditions for existence.] Zool. Inst. Akad. Nauk SSSR, 459 pp. Leningrad.

UTINOMI, H. 1954. The fauna of Akkeshi Bay. XIX. Littoral Pycnogonida. *Publ. Akkeshi Mar. Lab.*, No. 3, 28 pp.

1959. Pycnogonida of Sagami Bay. *Publ. Seto Mar. Biol. Lab.*, **7**(2): 197–222.

IV. APPENDIX

Tables for stations and localities from which pycnogonids have been collected.

1. Calanus stations records for Pycnogonida.

3, Coll. P-8, 29 VI 47, 58°50′N, 68°13′W, S Ungava Bay, 28 m, *Pseudopallene circularis*.

33, Coll. B-15, 10 VII 47, 59°13′N, 65°45′W, E Ungava Bay, 18–27 m, *Pseudopallene spinipes*.

44, Coll. P-51, 19 VIII 47, 60°23.5′N, 64°50′W, NE Ungava Bay, 80 m, from plankton tow at 40 m depth, *Nymphon brevitarse*.

129, Coll. P-28, 25 VIII 49, 58°43.3′N, 68°17′W, S Ungava Bay, 15–19 m, (plankton net on bottom), *Nymphon brevitarse*.

203, Coll. B-2, 8 VII 50, 58°50′N, 68°18′W, SW Ungava Bay, 30 m, *Nymphon grossipes*, *Eurycyde hispida*.

226, Coll. B-12, 13 VIII 50, 60°38′N, 64°38.9′W, Button Islands, entrance Hudson Strait, 90–100 m, *Nymphon brevitarse*.

319, Coll. B-2, 11 VIII 51, 62°21′N, 65°16′W, mouth Frobisher Bay, 68–118 m, *Nymphon grossipes*.

520, Coll. P-12, 4 VIII 53, 62°27′N, 79°51′W, N Mansel Island, NE Hudson Bay, 137 m, plankton tow at ca. 90 m, *Nymphon longitarse*.

549, Coll. B-16, 4 IX 53, 63°36′N, 82°00′W, Evans Strait, N Hudson Bay, 73–75 m, rock, *Nymphon robustum*.

612, Coll. B-7, 10 VIII 54, 63°06′N, 82°00′W, NE Coats Island, N Hudson Bay, 225 m, sand, small stones, *Nymphon robustum*.

613, Coll. B-9, 11 VIII 54, NE Coats Island, N Hudson Bay, 144–162 m, *Nymphon serratum*.

Coll. B-10, 11 VIII 54, same locality, 198 m, *Nymphon robustum*.

Coll. B-11, 11 VIII 54, same locality, 198 m, rock, *Nymphon hirtipes*, *N. stromi*.

711, Coll. B-10, 8 IX 55, 66°28′N, 86°12′W, Repulse Bay, 70–110 m, rock *Nymphon robustum*, *N. hirtipes*, *N. serratum*, *N. elegans*.

713, Coll. B-13, 12 IX 55, 66°55′N, 81°20′W, 5 miles S Cape Wilson, 25–49 m, rock, *Nymphon hirtipes*.

716, Coll. B-15, 19 IX 55, 69°23′N, 80°49′W, S Tern Island, 92–110 m, rock, *Nymphon hirtipes*, *N. grossipes*.

719, Coll. B-18, 29 IX 55, 69°20.5′N, 81°43.5′W, Hooper Inlet, 51 m, mud, *Nymphon megalops*.

722, Coll. B-19, 29 IX 55, 69°20′N, 82°00′W, Hooper Inlet, 36–45 m, mud, *Nymphon hirtipes*, *N. longitarse*.

723, Coll. B-41, 4 IX 56, 69°22.7′N, 81.44.3′W, Turton Bay, 22–24 m, mud and rock, *Nymphon hirtipes*, *Pseudopallene circularis*.

Spring 1956, Igloolik Island, from pool in surface ice, *Nymphon hirtipes*.

811, Coll. B-27, 17 VIII 56, 69°37.2′N, 81°06.3′W, Fury and Hecla Strait, 110 m, rock, *Nymphon robustum*, *N. serratum*.

Coll. B-28, 17 VIII 56, same locality, 106 m, plankton net on bottom, *Nymphon hirtipes*.

815, Coll. B-29, 18 VIII 56, 69°43.2′N, 82°07′W, Fury and Hecla Strait, 55 m, *Nymphon hirtipes*, *N. stromi*, *N. megalops*.

816, Coll. B-29, 18 VIII 56, 69°46.5′N, 82°07.5′W, Fury and Hecla Strait, 55–80 m, *Nymphon robustum*.

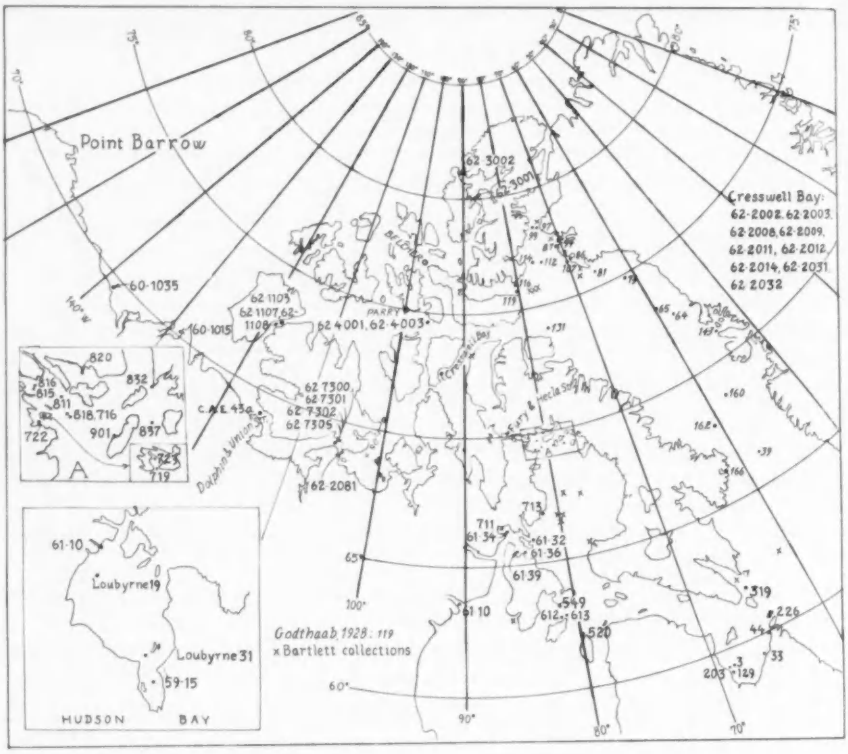


FIG. 11. Stations from which pycnogonids have been collected in American Arctic regions and western Greenland.

818, Coll. B-32, 26 VIII 56, 69°24′N, 80°53′W, S Tern Island, 95 m, mud and rock, *Nymphon robustum, N. hirtipes, N. megalops, Colossendeis proboscidea.*

820, Coll. B-34, 28 VIII 56, 69°55.7′N, 80°19′W, Murray Maxwell Bay, 73 m, mud, *Nymphon robustum, N. hirtipes.*

832, Coll. B-44, 8 IX 56, 69°44′N, 77°38.2′W, Koh Island to Cape Jensen, 79–90 m, sand and small stones, *Nymphon hirtipes, N. hirtum.*

837, Coll. B-45, 8 IX 56, 69°16′N, 77°48′W, Bray Island to Rowey Island, 45–55 m, sand and small stones, *Nymphon hirtipes, N. serratum.*

901, Coll. B-31, 26 VII 57, ca. 69°06′N, ca. 79°11′W, Frustration Bay, 10 m, sand and mud, plankton net on bottom. *Nymphon brevitarse.*

Coll. B-50, 24 VIII 57, same locality, 34 m, rock and mud. *Nymphon grossipes.*

59-15, Coll. B-13, 10 VII 59, 53°26′N, 79°52′W, James Bay, 55–60 m, mud, small stones, *Nymphon hirtipes, N. serratum.*

60-1035, 25 VIII 60, 69°32′N, 138°57′W, S Beaufort Sea, 22–44 m, mud, *Nymphon grossipes mixtum.*

61-10, Coll. B-9, 30 VII 61, 63°43′N, 91°43′W, Chesterfield Inlet, 75–90 m, rock, *Pseudopallene circularis.*

61-32, Coll. B-24, 14 VIII 61, 66°11′N, 84°12′W, SW Foxe Basin, 145 m, mud, rock, *Nymphon hirtipes.*

61-34, Coll. B-25, 23 VIII 61, 66°28′N, 86°16′W, Repulse Bay, 125 m, rock, sand, mud, *Nymphon hirtipes.*

61-36, Coll. B-26, 24 VIII 61, 65°32′N, 83°55′W, Frozen Strait, 285 m, mud, rock, *Nymphon hirtipes.*

61-39, Coll. B-44, 25 VIII 61, 65°32′N, 84°52′W, Duke of York Bay, 42 m, mud, rock, *Nymphon hirtipes.*

61-1015, 10 VII 61, 70°11′N, 128°35′W, S Beaufort Sea, 11 m, mud, sand, *Nymphon grossipes.*

62-1103, #4, 24 VII 62, 72°53′N, 118°01′W, Prince of Wales Strait, 26 m, *Nymphon robustum, N. longitarse.*

62-1107, #9, 26 VII 62, 72°53′N, 118°01′W, Prince of Wales Strait, 16–20 m, *Nymphon longitarse.*

62-1108, #11, 26 VII 62, 72°53′N, 118°01W, Prince of Wales Strait, 50 m, *Nymphon longitarse.*

62-2002, Coll. B-34, 4 VIII 62, 74°45′N, 94°04′W, Cresswell Bay, 40 m, clay, *Nymphon hirtipes.*

62-2003, Coll. B-23, 23 VII 62, 72°45.5′N, 94°07′W, Cresswell Bay, 35 m, gravel, *Nymphon sluiteri.*

62-2008, Coll. B-14, 3 VII 62, 72°45.6N, 94°04.5′W, Cresswell Bay, 30–45 m, sand *Nymphon robustum, N. hirtipes.*

Coll. B-15, 5 VII 62, 72°45.6′N, 94°04.5′W, Cresswell Bay, 30–45 m, sand, *Nymphon robustum.*

62-2009, Coll. B-26, 25 VII 62, 72°45′N, 94°04.5′W, Cresswell Bay, 35 m, clay, mud, *Nymphon robustum, N. hirtipes, N. sluiteri.*

62-2011, Coll. B-24, 23 VII 62, 72°45.3′N, 94°04′W, Cresswell Bay, 40 m, gravel, *Nymphon hirtipes, N. sluiteri.*

Coll. B-25, 24 VII 62, 72°45.3′N, 94°04′W, Cresswell Bay, 40 m, gravel, *Nymphon robustum, N. hirtipes, N. sluiteri.*

62-2012, Coll. B-27, 25 VII 62, 72°44.7′N, 94°05′W, Cresswell Bay, 36 m, clay, mud, *Nymphon robustum, N. hirtipes.*

62-2014, Coll. B-30, 25 VII 62, 72°44.1′N, 94°06′W, Cresswell Bay, 35 m, clay, *Nymphon robustum, N. hirtipes, N. sluiteri.*

62-2031, Coll. B-44, 11 VIII 62, 72°45.4′N, 94°13′W, Cresswell Bay, 40 m, clay, mud, *Nymphon robustum, N. hirtipes, N. sluiteri.*

62-2032, Coll. B-45, 11 VIII 62, 72°46.4′N, 94°15.2′W, Cresswell Bay, 59–62 m, clay, mud, *Nymphon robustum, N. hirtipes, N. sluiteri.*

Coll. B-46, same data as above, *Nymphon robustum, N. hirtipes.*

62-2081, Coll. B-3, 10 IX 62, 69°07′N, 105°10′W, S Victoria Island, *Nymphon hirtipes.*

62-3001, Coll. B-24, 22 VII 62, 80°00′N, 86°00′W, Eureka, 12–20 m, mud, *Nymphon robustum, N. sluiteri.*

Coll. B-27, 22 VII 62, same locality, 40–55 m, mud, *Nymphon robustum, N. sluiteri.*

Coll. B-30, 25 VII 62, same locality, 20 m, *Nymphon hirtipes, N. sluiteri.*

Coll. B-35, 27 VII 62, same locality, 30–45 m, mud, *Nymphon robustum, N. sluiteri.*

Coll. B-36, 27 VII 62, same locality, 2–30 m, mud, *Nymphon hirtipes, N. sluiteri.*

Coll. B-38, 27 VII 62, same locality, 2–20 m, mud, *Nymphon robustum.*

Coll. B-58, 12 VIII 62, same locality, 5–30 m, mud, *Nymphon hirtipes, N. sluiteri.*

62-3002, Coll. B-12, 11 VII 62, 81°05′N, 92°00′W, Nansen Sound, 3–5 m, mud, *Nymphon hirtipes*.
Coll. B-13, 11 VII 62, same locality, 15–20 m, mud, *Nymphon hirtipes*.

62-4001, Coll. B-45, 4 VIII 62, 74°36′N, 94°13′W, S Cornwallis Island, 35 m, *Nymphon micronyx*.
Coll. B-46, 6 VIII 62, same locality, 50 m, *Nymphon hirtipes*, *N.* spp. (unidentifiable fragments.)

62-4003, Coll. B-26, 17 VII 62, 74°37.5′N, 94°13′W, S Cornwallis Island, 25 m, *Nymphon microrhynchum*, *N. longitarse*.

62-7300, Coll. B-1, 23 VIII 62, 69°10′N, 106°20′W, S Victoria Island, 30 m, sand, *Nymphon robustum*, *N. hirtipes*.
Coll. B-2, 23 VIII 62, same locality, 30 m, mud, *Nymphon hirtipes*.

62-7301, Coll. B-3, 23 VIII 62, 69°10′N, 106°20′W, S Victoria Island, > 30 m, *Nymphon hirtipes*.

62-7302, Coll. B-4, 23 VIII 62, 69°10′N, 106°20′W, S Victoria Island, 50–60 m, mud, *Nymphon robustum*, *N. hirtipes*.

62-7305, Coll. B-5, 24 VIII 62, 69°10′N, 106°20′W, S Victoria Island, 20–30 m, rock, gravel, *Nymphon hirtipes*.

2. North American Arctic records for Pycnogonida, before 1947 (from Cole 1921; Hedgpeth 1943, 1948).

Parry Expedition, 1819–20, at North Georgia Island, approx. 75°N, 100°W, *Nymphon grossipes, N. hirtipes*; *Colossendeis proboscidea* (descr. by Sabine, 1827).

Parry Expedition, 1824–25, at Port Bowen, 73°14′N, 88°57′W, *Nymphon grossipes, N. hirtipes* (Ross, 1826).

Belcher Expedition, winter quarters, Northumberland Sound, 76°52′N, 97°W, *Nymphon hirtipes, Nymphon robustum* (described by Bell, 1855).

Canadian Arctic Exp., 1913–1918. St. 43a. 13 IX 15. Off Cockburn Point, Dolphin and Union Strait, 100 m, gray mud with pebbles, *Nymphon sluiteri, N. longitarse, N. hirtipes.*

Putnam-Baffin Land exp., 1927.

8 VIII 27, 45 miles east Cape Dorchester, Foxe Basin, *Nymphon elegans.*

10 VIII 27, 66°30′N, 80°W, Foxe Basin, *Nymphon grossipes, N. elegans, Pseudopallene circularis, Eurycyde hispida.*

12 VIII 27, 66°43′N, 80°07′W, Foxe Basin, 32–37 fathoms, *Nymphon elegans, N. megalops, Pseudopallene circularis, Eurycyde hispida.*

13 VIII 27, 66°46′N, 79°15′W, Foxe Basin, 34–37 fathoms, *Nymphon brevitarse, N. grossipes, N. serratum, Eurycyde hispida, Colossendeis proboscidea.*

24 VIII 27, 67°45′N, 79°09′W, Foxe Basin, 38 fathoms, *Eurycyde hispida.*

24 VIII 27, Center, Foxe Basin, 25 fathoms, *Eurycyde hispida.*

24/25 VIII 27, Center, Foxe Basin, 25 fathoms, *Nymphon grossipes, N. elegans, Pseudopallene circularis.*

25 VIII 27, Center, Foxe Basin, 25–31 fathoms, *Pseudopallene circularis.*

26 VIII 27, Center, Foxe Basin, 25–31 fathoms, *Nymphon grossipes, N. elegans, Eurycyde hispida.*

Hudson Bay Fisheries Expedition, 1930 (Loubyrne).

St. 19, 15 VIII 30, 61°11′N, 90°W, 136 m, mud, stones, *Nymphon hirtipes.*

St. 31, 22 VIII 30, 56°10′N, 82°21′W, 75 m, gravel, *Nymphon serratum.*

Norcross-Bartlett Expeditions, 1933, 1935, 1941. (Greenland records omitted.)

3 VIII 33, 63°10′N, 85°25′W, from floating seaweed, *Nymphon brevitarse.*

3 IX 33, Fury and Hecla Strait, 30 fathoms, *Nymphon hirtipes.*

St. 7, 3 VIII 35, 75°40′N, 78°50′W, 140–210 fathoms, gravel, *Nymphon hirtipes, N. elegans, Pseudopallene spinipes.*

St. 8B, 3 VIII 35, 75°40′N, 78°55′W, 150–200 fathoms, mud, *Nymphon sluiteri.*

4 VIII 35, 75°40′N, 78°59′W, 68–120 fathoms, rocky, *Nymphon grossipes.*

St. 17, 1941. Frobisher Bay, about 60 fathoms, *Nymphon longitarse.*

3. Pt. Barrow Stations 1948–50 (G. E. MacGinitie).

St. 10, 23 VIII 48, 150 ft, gravel, small stones, *Tanystylum anthomasti.*

St. 17, 9 IX 48, 80 ft, mud, *Achelia borealis.*

St. 20, 9 IX 48, 125 ft, stones (sea urchins, *Psolus*, sea anemones), *Nymphon grossipes, Achelia spinosa, Tanystylum anthomasti.*

St. 24, 16 IX 48, 110 ft, shells, pebbles, mud, *Pseudopallene circularis.*

St. 25, 8 VIII 49, 3 miles out, 120 ft, gravel, stones (large), mud, *Nymphon grossipes.*

St. 27, 9 VIII 49, 7 miles out, 420 ft, stones, gravel, *Nymphon grossipes, Pseudopallene circularis.*

St. 33, 30 VIII 49, 5 miles out, 184 ft, stones, boulders (*Psolus* and sea urchins, many), *Nymphon brevitarse, Pseudopallene circularis, Achelia spinosa.*

St. 35, 1 IX 49, 7.5 miles out, 328 ft, Gravel (coarse), stones (few large), *Achelia spinosa.*

St. 37, 6 IX 49, 7.5 miles out, 217 ft, stones, large perforated rocks, *Nymphon grossipes, Pseudopallene circularis, Achelia spinosa, Tanystylum anthomasti.*

St. 41, 6 X 49, 5 miles out, 295 ft, rocks, stones, gravel (*Psolus*), *Achelia spinosa.*

St. 42, 6 X 49, 4.3 miles out, 216 ft, rocks, stones (*Psolus* and sea urchins), *Nymphon grossipes, N. brevitarse, Oropallene polaris, Achelia spinosa.*

St. 43, 6 X 49, 4 miles out, 213 ft, gravel, mud, *Nymphon grossipes.*

St. 44, 11 X 49, 8 miles out, 453 ft, rocks, stones, gravel (small amount), *Psolus, Pseudopallene circularis, Achelia spinosa.*

St. 45, 11 X 49, 6 miles out, 341 ft, rocks (few), stones, gravel (sea urchins), *Pseudopallene circularis, Achelia spinosa.*

St. 46, 14 X 49, 6 miles out, 152 ft, stones, mud, rocks (few), *Nymphon brevitarse.*

St. 47, 14 X 49, 4 miles out, 175 ft, gravel, stones (small) (sea urchins), *Nymphon grossipes, N. brevitarse, Pseudopallene circularis, Achelia spinosa, A. borealis.*

St. 50, 18 II 50, 3.2 miles out, 162 ft, mud, gravel, stones, rocks (few small), (haul made by dog team), *Achelia spinosa.*

Washed ashore: *Nymphon grossipes, N. brevitarse, N. Longitarse* (no other collections of this species by MacG.!), *Achelia borealis.*

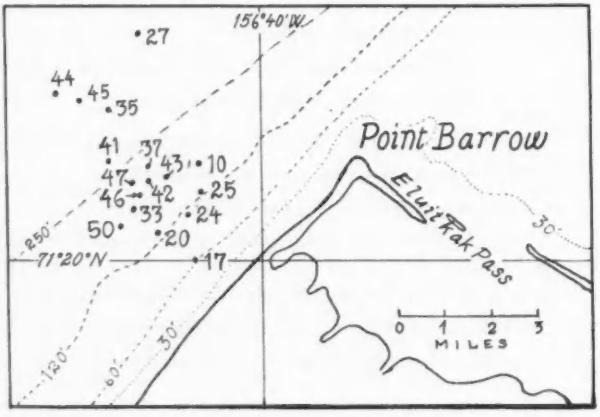


FIG. 12. Stations off Point Barrow from which pycnogonids have been collected (from MacGinitie, 1957).

OBITUARY

Edith Berkeley

1875 — 1963

Mrs Cyril J. (Edith) Berkeley died on February 25, 1963, in Nanaimo, British Columbia. While she was never a member of the staff of the Fisheries Research Board of Canada, she became such an integral part of the Nanaimo Biological Station that her passing has left a void and a break, nearly the last, with the very early story of the Station.

Mrs Berkeley's father, Alfred Dunington, a civil engineer of Yorkshire descent, was one of the outstanding specialists in bridge-building of his generation. He was engaged in such a project at Tulbagh, South Africa, when Edith was born there on September 1, 1875. Her mother, who was of Cornish origin, took her to England as soon as she was old enough to stand the cross-country journey to the coast in a bullock-wagon and her early childhood was spent there, with her mother and grandmother, until she was about 5 years old. Her father, meanwhile,

had transferred from Africa to India and, at that age, she was taken by her mother to Lower Bengal to join him. In due course, the climate began to tell and it became necessary to move to more temperate conditions. The family migrated to Tasmania. At the age of 14 years she travelled unaccompanied from Tasmania, via New Zealand and Cape Horn, to England on one of the old Shaw-Saville sailing ships—a long and eventful voyage for one so young.

In England she was sent to the Wimbledon high school whence she matriculated in the University of London at about the age of 18 and was awarded a scholarship to enable her to go on to university. Her intention at this time was to take up medicine and she did, indeed, complete a full pre-medical course, but, after 2 or 3 years, she had made up her mind to devote herself to pure science. She enrolled in the chemical and zoological departments at University College, London, in 1895. This was a notable year in chemistry there. Argon had been discovered by Sir William Ramsay the previous year and, in 1895, this was followed by his isolation of helium. These two discoveries led, during the following years, to that of the whole series of inert atmospheric gases on which Ramsay's fame rests. Mrs Berkeley was always happy to have been closely associated with these events. In recent years she, and one other, were the last surviving members of that group of staff and students, the "one other" being her husband. She and her husband met in Ramsay's research laboratory in 1898. They were married in 1902. In zoology Mrs Berkeley worked under Professor Weldon and, due largely to his influence, developed an interest in the comparative anatomy of polychaetes. Marriage, however, interrupted zoological studies, which remained in abeyance until resumed at Nanaimo 18 years later.

In 1902, Mrs Berkeley returned once again to India where her husband had received an appointment under the Government of Bengal to carry out work designed to aid the natural indigo industry to resist the competition of the synthetic dye then coming on the market. This took them to northern Bihar, the seat of the indigo industry in India, and there they remained for the next 11 years. During this time Mrs Berkeley assisted in the chemical work involved in her husband's investigations and made several visits to England to see her mother and young daughter (born 1903) who had been left in the care of her grandmother at an early age. In 1913, Mr and Mrs Berkeley visited British Columbia on their way back to England and were so attracted by the country that they decided to return there and take up farming in the Okanagan Valley. This they did early in 1914.

Two years of it were sufficient to persuade them that they were misplaced as farmers and for them to feel the call to more scientific interests. The University of British Columbia was then developing and there were opportunities for appointments in many departments. Mrs Berkeley assisted Dr Andrew Hutchinson in starting zoology courses. This she did during the next few years and the work led to her first visit to the Biological Station at Nanaimo for the purpose of collecting material for courses in 1917. In 1919 she and her husband moved over to the Station permanently, he having accepted an assistantship under Dr C. McLean Fraser there, and she having been offered facilities to carry on zoological research as a volunteer investigator. Her original intention had been to carry on the comparative anatomy and physiological studies on polychaetes begun more than 20 years previously under Professor Weldon, but she found the taxonomy of the group on the coast in so chaotic a condition that she was obliged to do something about it in the first place. This led to extended taxonomic studies including that on material sent her from farther afield and, ultimately taxonomy filled her time. For the first 12 years or so she worked alone, but later the pressure became so heavy that Mr Berkeley was called into co-operation and they worked and published jointly thereafter. Between 1923 and 1962 some 40 publications appeared.

In 1951, Mrs Berkeley's only offspring, Alfreda (Mrs A. W. H. Needler), died. This was a terrific shock to her but after a year or so she mostly regained her spirit and carried on her research with vigour. Through her thorough and diligent work she established herself as a world authority in polychaete systematics.

Outside her scientific work Mrs Berkeley's major interest was in her garden. She and her husband had purchased a house, built by the Reverend George W. Taylor, the first director of the Biological Station, when they first settled in Departure Bay. This had a rather extensive garden which had been little developed and they made it their business to make the most of it during the years which followed. Mrs Berkeley was particularly interested in the species of *Rhododendron*, of which a very large collection now exists in the garden; many of them are unique specimens in size and age on the west coast of North America.

Mrs Berkeley was an unassuming, kindly gentlewoman who has left the stage where she made a name for herself in her science and her garden, all the while maintaining a keen interest in world events and good literature.—W. A. CLEMENS.

NOTES

An Occurrence of Mako Sharks, *Isurus oxyrinchus*, Rafinesque 1810, in the Canadian Atlantic

The capture of sharks nearly always attracts attention but frequently they are wrongly identified. Scattergood (1962) in reporting the first record of the mako shark in Maine waters wrote "The capture of mako sharks has been reported repeatedly along the Maine coast; however, there have been no published authentic records of their occurrence north of Cape Cod . . . Of the many "mako" landings that I have investigated in Maine, only one was *Isurus oxyrinchus* . . . harpooned July, 1957, off Boon Island, York County . . . ".

During the summer of 1962, two mako sharks were caught from the Fisheries Research Board of Canada vessel, M. V. *Harengus*, on Browns Bank. They are apparently the first authentic records of occurrence of mako sharks in Canadian Atlantic waters.

The two specimens were caught on August 5 and 8 using a surface longline with a no. 9 Mustad tuna hook baited with mackerel, on the Peak of Browns Bank (approximate Lat. 42°10′N, Long. 65°40′W). One was a male (189 cm total length weighing 79.8 kg) and the other a female (213 cm total length weighing 74.8 kg). The lower jaws of both specimens were preserved and are stored (catalogue No. 22114) at the Royal Ontario Museum, Toronto, Ontario.

Proportional dimensions in percent of total length (cf. Bigelow and Schroeder, 1948) for the two specimens (189 and 213 cm long, respectively) are listed below. All measurements except fin margins were made as straight lines between points.

Snout length in front of: Nostrils 5.0, 4.9; eye 6.7, 7.4; mouth 7.0, 6.0
Snout to origin of: Pectoral 30.2, 27.7; first dorsal 34.2, 39.0; anal 84.2, 74.4; caudal 88.3, 82.3
First dorsal fin: Vertical height 13.3, 10.1; base length 10.1, 9.2
Anal fin: Vertical height 2.0, 2.1; base length 1.8, 0.9
Caudal fin: Upper margin 25.7, 21.4; lower margin 18.8, 17.0; peduncle width 7.4, 9.5; peduncle depth 2.3, 2.4
Body at origin of pectoral: Breadth 15.4, 12.8; depth 13.4, 11.9
Interspace between: First and second dorsals 29.9, 25.1; second dorsal and caudal 8.2, 8.6; anal and caudal 9.1, 7.6
Pectoral fin: Length anterior margin 19.1, 19.0
Nostrils: Distance between inner ends 4.0, 4.4
Eye: Horizontal diameter 1.8, 1.5
Mouth: Width 7.7, 7.4

Scattergood (1962) stated "there are no Canadian Atlantic records of the mako". Bigelow and Schroeder (1948) indicate that the northern limit of its distribution in inshore waters is at about Cape Cod. They stated, however, that "it would not be astonishing if it were encountered farther north, offshore, in the sweep of the Gulf Stream, although there is as yet no positive record of it either from the Nova Scotian Banks or from the Banks of Newfoundland". They also stated "it rarely if ever occurs in water colder than about 60°F (15.6°C)".

J. Fish. Res. Bd. Canada, **20**(5), 1963.
Printed in Canada.

The captures recorded here were made on Browns Bank shoreward of the Gulf Stream and thus extend the known range of the species some 200 miles to the north and east.

The two specimens were caught respectively where the surface water temperatures were 15.8 and 16.1°C and the bottom water temperatures 7.3 and 9.2°C. Surface salinities were 32.02 and 32.29‰.

The makos were taken along with specimens of the porbeagle, *Lamna nasus* (Bonnaterre) 1788, which ranges north to the southwestern Gulf of St. Lawrence (Bigelow and Schroeder, 1948; McKenzie, 1959). Both species belong to the mackerel shark family and because of their similarity in appearance must be examined carefully for positive identification. According to Bigelow and Schroeder (1948) a vertical line from the origin of the dorsal fin falls behind the pectoral fin in the mako shark whereas in the porbeagle it falls well forward of the posterior margin of the pectoral fin.

Both the mako and the porbeagle have a well-developed lateral keel on each side of the caudal peduncle. They may be distinguished, however, in addition to the dorsal fin position, by the secondary keel that is present on the upper part of the lower lobe of the caudal fin of the porbeagle. This secondary keel is located immediately below the posterior portion of the primary keel. The mako has no secondary keel. The lower jaw of the mako (Fig. 1) is longer and narrower than that of the porbeagle (Fig. 2). Also, the teeth of the mature porbeagle have pronounced lateral basal cusps that are not present on mako teeth (see also Bigelow and Schroeder, 1948). This latter character, however, is less reliable on small specimens. We have on hand a female porbeagle, 118 cm in total length (ROM cat. No. 22042), in which the functional rows of teeth in both jaws show no evidence of lateral cusps, but some of the teeth in the first replacement row of the upper jaw do have obvious lateral cusps. On the basis of tooth characters this specimen could be easily mistaken for a mako shark and, in fact, this was our initial identification. (J. A. F. Garrick, U.S. National Museum, very kindly assisted in the correct identification.) Thus, although the tooth character may be most useful and reliable for the identification of adult porbeagles and makos, caution must be exercised when dealing with juvenile specimens of the order of 100 cm total length or less.

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

S. N. TIBBO
R. A. MCKENZIE

The Royal Ontario Museum
University of Toronto, Toronto 5, Ontario

W. B. SCOTT

Received for publication April 10, 1963.

REFERENCES

BIGELOW, H. B., AND W. C. SCHROEDER. 1948. Fishes of the Western North Atlantic. Pt. 1, *Mem. Sears. Found. Mar. Res.*, No. 1, 576 pp.

MCKENZIE, R. A. 1959. Marine and freshwater fishes of the Miramichi River and Estuary, New Brunswick. *J. Fish. Res. Bd. Canada*, **16**(6): 806–833.

SCATTERGOOD, LESLIE W. 1962. First record of mako, *Isurus oxyrinchus*, in Maine waters. *Copeia* for 1962, No. 2, p. 462.

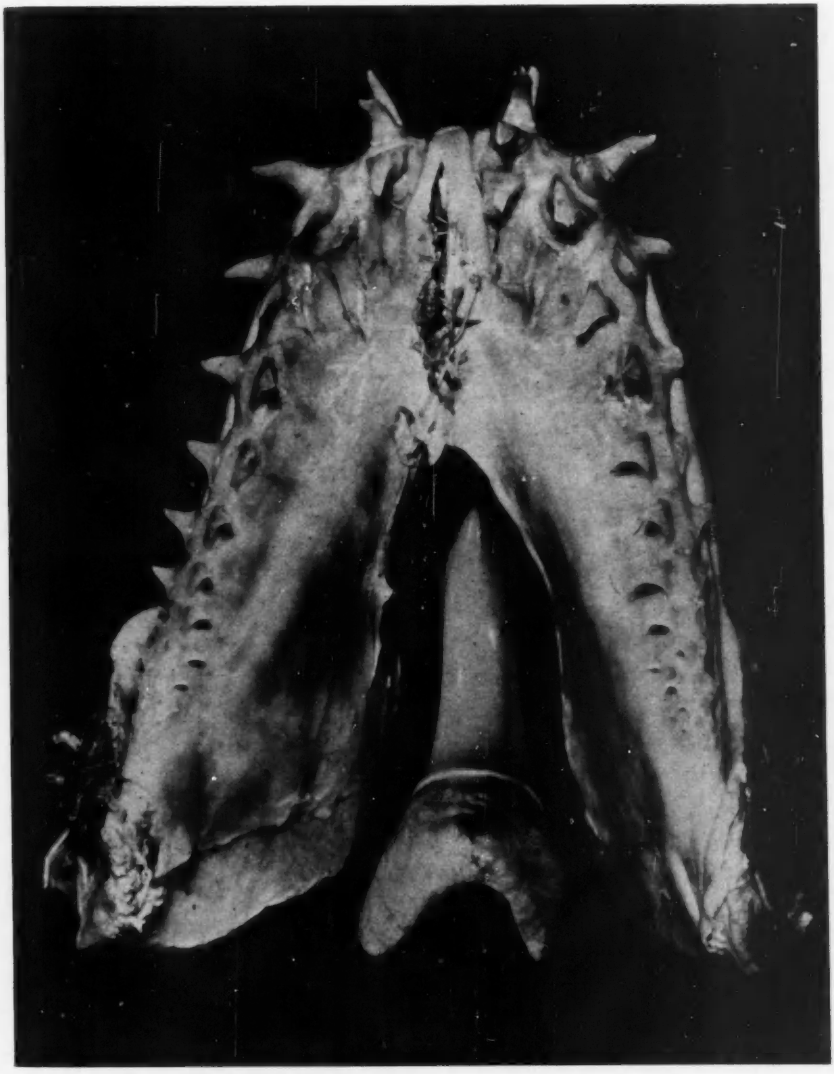


FIG. 1. Lower jaw of mako shark, *Isurus oxyrinchus*. Inset shows enlarged photograph of a mako tooth with no lateral basal cusps.

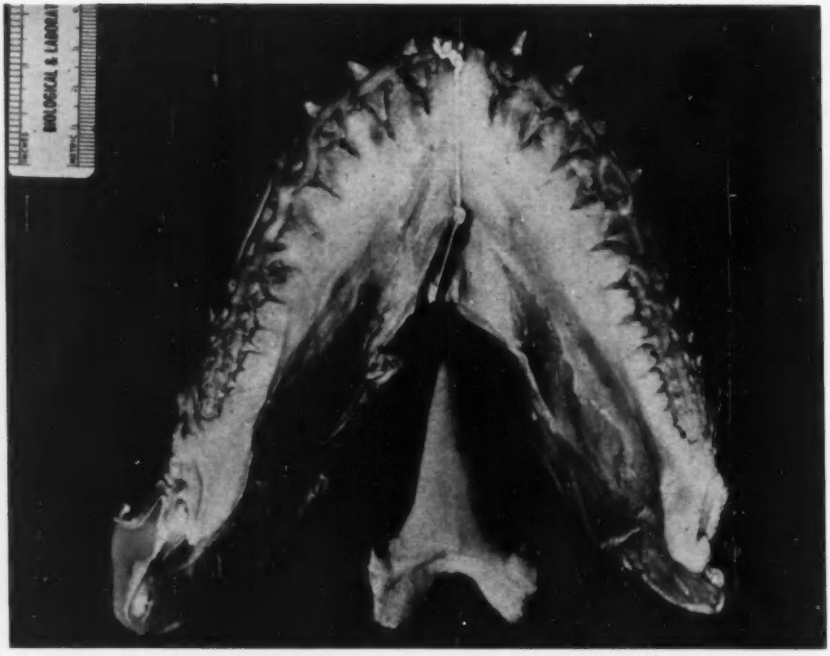


FIG. 2. Lower jaw of porbeagle shark, *Lamna nasus*. Inset shows enlarged photograph of a porbeagle tooth with pronounced lateral basal cusps.

RECENT ARTICLES ON INVESTIGATIONS OF THE FISHERIES RESEARCH BOARD OF CANADA PUBLISHED IN OTHER PERIODICALS

Studies No.

776. **Grajcer, Dov, and D. R. Idler.** 1963. Conjugated testosterone in the blood and testes of spawned Fraser River sockeye salmon (*Oncorhynchus nerka*). Canadian J. Biochem. Physiol., **41**(1): 23–30.

777. **Stephens, K.** 1962. Improved tripping mechanism for plastic water samplers. Limnol. Oceanog., **7**(4): 484.

778. **Stephens, K., and J. D. H. Strickland.** 1962. Use of a thermopile radiometer for measuring the attenuation of photosynthetically active radiation in the sea. Limnol. Oceanog., **7**(4): 485–487.

779. **Saunders, J. W., and M. W. Smith.** 1962. Transplantation of brook trout (*Salvelinus fontinalis* (Mitchill)) within a small stream system. Trans. Am. Fish. Soc., **91**(4): 388–394.

780. **Odense, Paul H., and C. W. Shinners.** 1962. Direct vertical starch gel electrophoresis of cod muscle tissue. Canadian J. Biochem. Physiol., **40**(12): 1842–1843.

781. **Dyer, W. J., D. I. Fraser, D. G. Ellis, D. R. Idler, W. A. MacCallum and E. Laishley.** 1962. Quality changes in stored refrozen cod fillets. International Institute of Refrigeration, Supplement to the Bulletin, 1962–1, pp. 515–524, Washington, D.C.

782. **Ackman, R. G., R. D. Burgher, J. C. Sipos and P. H. Odense.** 1962. Carbonaceous fouling of catherometer filaments. J. Chromatog., **9**(4): 531–534.

783. **Lawler, G. H.** 1963. Using the trammel net in Canadian waters. Canadian Fisherman, **50**(8): 17–20.

784. **Templeman, Wilfred.** 1961. Summary of research work carried out in Subarea 2 [of the ICNAF Convention Area] in 1960. Int. Comm. NW Atlantic Fish., Standing Committee on Research and Statistics, Proceedings and Selected Reports, 1961 Annual Meeting, pp. 103–104.

785. **Templeman, Wilfred.** 1961. Summary of research work carried out in Subarea 3 [of the ICNAF Convention Area] in 1960. Int. Comm. NW Atlantic Fish., Standing Committee on Research and Statistics, Proceedings and Selected Reports, 1961 Annual Meeting, pp. 105–107.

(Continued on next page)

786. **Sandeman, E. J., and A. W. May.** 1961. Preliminary results of experiments on the measurement of meshes with different gauges and by different operators. Int. Comm. NW Atlantic Fish., Standing Committee on Research and Statistics, Proceedings and Selected Reports, 1961 Annual Meeting, pp. 123–144.

787. **Templeman, W.** 1962. Summaries of research, 1961. Subareas 2 and 3 [of the ICNAF Convention Area]. Int. Comm. NW Atlantic Fish., Annual Proceedings for 1961–62, Vol. 12, pp. 23–30.

788. **Templeman, W.** 1962. Canadian research report, 1961. Subareas 2 and 3 [of the ICNAF Convention Area]. Int. Comm. NW Atlantic Fish., Redbook 1962, Part II, Summaries of Research for 1961, pp. 3–20.

789. **Martin, W. R.** 1962. Canadian research report, 1961. Subareas 4 and 5 [of the ICNAF Convention Area], Biology. Int. Comm. NW Atlantic Fish., Redbook 1962, Part II, Summaries of Research for 1961, pp. 21–27.

790. **Lauzier, L. M.** 1962. Canadian research report, 1961. Subareas 4 and 5 [of the ICNAF Convention Area], Oceanography. Int. Comm. NW Atlantic Fish., Redbook 1962, Part II, Summaries of Research for 1961, pp. 28–30.

791. **Templeman, Wilfred.** 1962. Divisions of cod stocks in the northwest Atlantic. Int. Comm. NW Atlantic Fish., Redbook 1962, Part III, Selected Papers from the 1962 Annual Meeting, pp. 79–123.

792. **May, A. W., and V. M. Hodder.** 1962. Comparisons of ICNAF and Westhoff gauges under field conditions. Int. Comm. NW Atlantic Fish., Redbook 1962, Part III, Selected Papers from the 1962 Annual Meeting, pp. 141–153.

793. **Sandeman, E. J., and A. W. May.** 1962. Comparative effects of gauge pressure on mesh size measurements of manila nets. Int. Comm. NW Atlantic Fish., Redbook 1962, Part III, Selected Papers from the 1962 Annual Meeting, pp. 154–180.

Copies of individual reprints, if available, may be obtained from the authors or Board establishments through which the investigations were conducted.

Reprints of these articles are included in an annual volume of "Studies", which is distributed to a selected mailing list. (Articles numbered 689 to 775 appeared in the 1962 Studies.)

PRINTED PUBLICATIONS OF THE FISHERIES RESEARCH BOARD OF CANADA

The following publications are for sale by the Queen's Printer, Ottawa, Canada. All remittances must be in advance, payable in Canadian funds to the order of the Receiver General of Canada, and sent with order to the Queen's Printer. These publications may be consulted at the library of any of the Board's establishments.

Journal of the Fisheries Research Board of Canada

Subscription to annual volume of six bi-monthly issues, post-paid (Canada, United States, Mexico), $6.50; single issues $2.00. To other countries, post-paid, $7.75 and $2.25. This present issue 20(5) was published October 31, 1963.

Annual Reports of the Fisheries Research Board of Canada

Reports of the work carried on under the direction of the Board, including a list of scientific staff and of all publications issued during the preceding calendar year.

Report for the fiscal year ended March 31, 1962. (1962, 205 pp., 75 cents.)

Bulletins of the Fisheries Research Board of Canada

Published irregularly, each dealing in technical or popular style with a particular subject of the Board's work.

No. 110. Index and list of titles, publications of the Fisheries Research Board of Canada, 1901–1954. By Yvonne Bishop, Neal M. Carter, Dorothy Gallus, W. E. Ricker and J. Murray Speirs. (1957, 209 pp., $1.00.) (*A circular entitled "Lists of titles of publications of the Fisheries Research Board of Canada, 1955–1960" prepared by R. L. MacIntyre, is available free of charge from the Fisheries Research Board, Ottawa.*)

No. 126. (*Édition française*) Entreposage et transport du poisson en eau de mer réfrigérée. Par S. W. Roach, J. S. M. Harrison et H. L. A. Tarr. (1963, 71 pp., 75 cents.)

No. 135. Giant scallops in Newfoundland coastal waters. By H. J. Squires. (1962, 29 pp., 75 cents.)

No. 136. Osteological studies on Pacific salmon of the genus *Oncorhynchus*. By Vadim D. Vladykov. (1962, 172 pp., $2.50.)

No. 137. Seals of arctic and eastern Canada. By A. W. Mansfield. (1963, 30 pp., $1.30.)

No. 138. Antibiotic dips for preserving fish fillets. By C. H. Castell and Jacqueline Dale. (1963, 70 pp., $1.30.)

No. 139. A review of the Strait of Georgia trawl fishery. By C. R. Forrester and K. S. Ketchen. (1963, 81 pp., $1.75.)

Second edition of Bulletin No. 68. Fishes of the Pacific Coast of Canada. By W. A. Clemens and G. V. Wilby. (1961, 443 pp., $6.50 cloth-bound.)